THE UNIVERSITY OF KANSAS
SCIENCE BULLETIN

Vol. 53, No. 3, pp. 121-182 June 20, 1986

Larvae of the Crane Fly Genus *Tipula* in North America (Diptera: Tipulidae)[1]

Jon K. Gelhaus

Department of Entomology, University of Kansas

Contents

[1] Contribution No. 1948 from the Department of Entomology, The University of Kansas, Lawrence, Kansas, 66045, U.S.A.

ABSTRACT

This is a taxonomic study concerning larvae of the crane fly genus *Tipula*. Descriptions and illustrations are given for larvae of at least one species in 20 of the 27 recognized nearctic subgenera; for four of these groups, larvae are described for the first time. A key is presented to the subgenera of *Tipula* and to certain similar genera for final-instar larvae. External morphology, concentrating on the diversity found among the subgenera, and various rearing methods are discussed. Included in each subgeneric treatment is a discussion of the characters of the group, and a list of known habitats.

Larvae of *Tipula* occupy a wide range of aquatic to terrestrial situations and the morphology correspondingly varies among the subgenera. Overall, larval groups are in agreement with the adult subgeneric classification, although the subgenus *Trichotipula* contains two extremely different types of larvae. No unique characters of the larvae were found to unify the entire genus, but certain groupings of subgenera have distinctive sets of characters. Some groups within the genus are more similar morphologically to other tipuline genera, such as *Holorusia* and *Prionocera*, than to many other subgenera of *Tipula*.

INTRODUCTION

At the time of Alexander's comprehensive 1920 paper, "The Crane-flies of New York. Part II. Biology and Phylogeny," the larvae of only four percent (16 species) of the nearctic species of *Tipula* had been described. From 1920 to 1983, the larvae of only five additional nearctic species were described and illustrated, and the life history of only one species was studied in any detail. My work represents a step toward correcting this lack of knowledge about this diverse genus, including descriptions of larvae and information about their biology.

The cosmopolitan genus *Tipula* contains approximately 450 nearctic species placed in 27 subgenera (Alexander, 1965). *Tipula* larvae are by nature of their habitat inconspicuous, although the larval stages may last from six months to five years. Larvae can be sufficiently abundant locally to have an appreciable ecological impact. The larval habitats vary tremendously within the genus. Larvae of some species are fully aquatic and are found in leaf packs or on the bottoms of streams (e.g., *Nippotipula*), while others occur in the wet soil of stream and lake margins, seepages, algal mats or wet mosses (e.g., *Yamatotipula*). Many species such as those in *Lunatipula* are found in soil under layers of leaf mold or other decaying vegetation in forested areas. Some species (e.g., *Serratipula*) are in the soil of pastures or meadows, where they feed on roots and leaves of young grasses. A few of these may become pests in favorable years by denuding hundreds of acres of rangeland, thus earning the common name "range crane fly." Some larvae are found in dead wood at various stages of decay (e.g., *Pterelachisus*). Still others, such as *Eremotipula* (inferring from pupal collections), occur in semiarid areas in the soil under rabbitbrush *(Chrysothamnus)* and other shrubs. All species appear to be herbivorous or to feed on decaying plant matter.

Existing keys, most recently by Alexander and Byers (1981), will at best identify larvae of nearctic *Tipula* to the generic level, and certain species of *Tipula* cannot even be distinguished from other genera of Tipulinae by these keys. All 42 subgenera are based exclusively on adult characters, and in the present study, inconsistencies are seen between adult and larval groupings in certain subgenera (e.g., the two larval types of the subgenus *Trichotipula*).

I have examined reared material for as many species as possible (approximately 70 species, 16 percent of the genus in the Nearctic) to ascertain the characters for each subgenus. Larvae were obtained for 20 of the 27 nearctic subgenera, and for four of these subgenera *(Bellardina, Hesperotipula, Serratipula* and *Sinotipula)* the larvae are here described for the first time. A key to the subgenera is included, as well as information on larval biology.

Acknowledgements

I thank G. W. Byers, who suggested this project and has provided advice and support on numerous occasions, particularly in editing drafts of this paper.

Reared and associated larvae and adults of *Tipula* are not often encountered in museum collections; therefore, everyone who contributed specimens has added significantly to this work. The collection of J. Speed Rogers at the University of Michigan (UM), Ann Arbor, contains many specimens reared by Rogers; it also includes the specimens used by C. P. Alexander in his 1920 paper. I thank T. E. Moore, curator of the Michigan collection, for the loan of this important material. Thanks also go to H. J. Teskey, Canadian National Collection (CNC), Ottawa, for the use of his extensive collection from eastern North America. I also used specimens from the following museums: Dept. of Entomology, American Museum of Natural History (AMNH), Entomology Museum, University of California at Riverside (UCR), Entomological Museum, North Carolina State University (NC) and the James Entomological Collection, Washington State University (WSU). Other specimens are from the Snow Entomology Museum, University of Kansas (KU), State Biological Survey of Kansas collection (SBSK), and from my personal collection (JKG). Other individuals provided certain species or other help and deserve acknowledgement: S. A. Teale (ST), State University of New York, Syracuse, identified many of my reared adult *Tipula* from the Rocky Mountains and loaned specimens of *T. platymera;* G. Pritchard (GP), University of Calgary, Alberta, sent specimens of *T. commiscibilis* and *sacra;* F. B. Brodo, Carleton University, Ottawa, loaned larvae of the genus *Prionocera*, which allowed me to separate *Prionocera* from the subgenus *Angarotipula;* H. M. Knizeski (HK), Mercy College, Dobbs Ferry, New York, provided specimens of *T. ignobilis;* and P. Oosterbroek, Institute of Taxonomic Zoology, University of Amsterdam, spent a number of hours helping me translate the 1957 paper of B. Theowald. Financial costs for museum visits and fieldwork were partially defrayed by two awards from the Raymond H. Beamer Memorial Fund, University of Kansas.

I would like to especially thank the staff of the State Biological Survey of Kansas for the use of certain equipment and supplies throughout the period of this study, to C. D. Michener and two anonymous reviewers for their helpful comments, and to C. W. Young, now of the Carnegie Museum, Pittsburgh, who spent many hours helping me locate larvae in the field during the initial phase of this study.

Finally, and most importantly, I would like to express my appreciation to my wife, Evalyn, for her patience and constant encouragement.

Materials and Methods

Larvae of 68 species of *Tipula* and of *Holorusia rubiginosa* and *Prionocera dimidiata* were examined. I have reared 37 of these species one or more times. I collected larvae primarily in eastern Kansas, northern New Mexico and central California; most other collections studied were made in eastern North America.

The diversity of habitats occupied by larvae of *Tipula* requires a variety of collection methods. Details are given by Gelhaus (1983). A sturdy garden trowel is indispensable for collecting in aquatic and terrestrial situations. Uses include clearing aside soil in forest situations; digging up saturated soils bordering aquatic habitats for sieving; or dislodging gravel and rocks on the bottom of fast-flowing streams and rivers. Both a D-frame aquatic net and forceps have limited use when collecting larvae of *Tipula*. The D-frame net is desirable when larvae inhabit leaf packs (e.g., *Nippotipula*) or are under rocks in rivers and streams (e.g., *Sinotipula*). Heavy forceps are needed for hand collecting in aquatic habitats that are too small for D-nets or sieves, such as shallow seepages or springs. Detailed examination of mosses or soft, rotting logs requires forceps.

As briefly discussed by Brindle (1960c), the use of a sieve when collecting in saturated soils is highly recommended, as larvae are cryptically colored, slow moving and easy to overlook when only hand collecting with forceps. A 1 mm mesh screen is adequate for retaining all late-second instar and older larvae (Brindle suggests $^1/_{16}$ of an inch). When sieved, a larva usually curls up for a short time, or if small and very active, it may move through the sieve mesh. A sieve works best in fine, sandy areas; it is not as efficient in heavily organic areas with large amounts of plant debris. In all cases, though, sieving reduces the amount of material to be sorted through and washes debris from the larvae, making them more visible.

Terrestrial and semiaquatic larvae almost always live within 50 mm of the substrate surface, regardless of climatic conditions. Larvae of the related genus *Dolichopeza* remain near the surface even during the winter when their habitat is frozen (Byers, 1961), and I have observed similar behaviors in larvae of the subgenera *Luna-*

tipula, Pterelachisus and *Vestiplex*. Hot, dry summer weather also does not appear to force larvae to move deeper into the substrate. *Tipula (Trichotipula) stonei,* in fact, develops and matures during the summer, and even during a prolonged drought, larvae were found in the top 30-50 mm of dry forest soil. *Tipula (Lunatipula) oxytona* moves downward to 200 mm during dry periods (Rogers, 1933), but this appears to be an exceptional instance and may be related to this species' occurrence in sandy soils which rapidly lose moisture near the surface.

For species whose larval habitat is unknown, certain predictions can be made by observing the behavior of the adults or by knowledge of larval habitats for related species. Adults may occur away from the specific larval habitat. Teneral adults or ovipositing females give a clearer idea of where larvae occur, as does the activity of males seeking newly emerged females. Pupal collections are useful, for pupae occur near the larval habitat or even among the larvae. In species with highly synchronous adult emergences, however, once pupae are found, few individuals will remain as larvae, and a return visit is required during the next generation to secure larvae.

Snap-cap glass vials (60 ml), one-third filled with soil or other habitat material and each with only one or two larvae, are excellent for field use and allow larvae to be easily recovered once in the laboratory. Self-sealing plastic bags are excellent for transporting larvae over a long time period, when many larvae are found in one specific site, or if associated soil or debris from the larval habitat is needed for rearing or sieving in the laboratory. The bags should be one-third to one-half filled with substrate from the larval habitat. The collections are then kept cool until brought into the laboratory, as even short periods of heat (as in a vehicle on a warm day) will kill the larvae. Larvae from aquatic habitats should be transported in damp debris, mosses or leaf litter; although from an aquatic habitat, they are susceptible to drowning.

A single microhabitat may yield more than one species of larvae; therefore, larvae should be carefully sorted before placement in rearing chambers. Larvae often expose the spiracular discs at the surface when placed in water, permitting identification in life with a microscope. Chilling the larvae for a few minutes helps if they are very active.

A proper rearing container must admit fresh air and maintain an even moisture level. Both Chiswell (1956) and Byers (1961) recommended Petri dishes, but I found such dishes of limited use. Petri dishes have a small volume, are easily kept too wet, but also quickly dry out. The small volume also allows overcrowding even when there are only a few larvae per dish. Petri dishes are advantageous for observations of larval behavior, but for rearing, I prefer glass containers 40-80 mm high and 100 mm diameter. Such jars hold enough food (i.e., leaf litter, rotting wood, etc.) from the habitat to allow late-third or fourth-instar larvae to develop to the pupal stage. Moreover, they do not require daily checking for food depletion and moisture control. Aquatic species need only wet litter or, at most, a small amount of free water; terrestrial species should be kept just damp. Ideally, one larva should be kept per container; practically, I have kept up to six larvae per jar.

All *Tipula* reared have been herbivorous or saprophagous. Wet, decaying leaves for aquatic species and damp leaves or debris for terrestrial larvae suffices for most; some species of *Yamatotipula, Platytipula* and *Triplicitipula* will accept and feed readily on young green shoots of common weeds (Young, 1981; Gelhaus, personal observation). When conditions are adequate, larvae remain buried within the debris or soil during the day.

Although in most cases it is best to try to duplicate the natural conditions of the larval habitat in the laboratory, in some situations this is not desirable. It is not necessary to maintain species from rapidly flowing streams or rivers, such as some *Sinotipula* or *Nippotipula,* in constantly aerated water. Gordon Pritchard *(in litt.)* reared larvae of *T. (Sinotipula) commiscibilis* in containers of wet leaves at 15 degrees C., although they were originally collected from a fast-flowing, cold, mountain stream. Many species are influenced by photoperiod, particularly when about to pupate; they should be exposed to a source of natural light or to artificial light of similar periodicity (e.g., *Platytipula*).

Since a female *Tipula* may lay 200-300 eggs, rearing larvae from eggs would appear to be ideal for obtaining many larvae of a single species. Unfortunately, the life histories of many species cause problems in rearing and in maintaining laboratory cultures. Some mated females are reluctant to lay. Although pinching the cervical region of the female will often induce egg laying, it is not reliable. Eggs of many species undergo an obligate diapause that is broken only when they are exposed to certain photoperiods, temperatures or moisture conditions. For example, Hartman and Hynes (1977) found that the eggs of *T. (Triplicitipula) simplex* would only hatch after exposure to a certain photoperiod and alternating wet and dry conditions. I found that eggs of an undescribed

species of *T. (Platytipula)* only hatched after exposure to cold and typical winter photoperiods. Other groups have eggs which hatch soon after being laid (approximately one week). Subgenera with brief egg stages include *Nippotipula, Bellardina* and most species of *Yamatotipula*. Eggs of *T. (Nobilotipula) nobilis* had no apparent diapause but took approximately three weeks to hatch. Eggs of *Lunatipula, Pterelachisus* and *Savtshenkia* appeared to have a developmental diapause but the cues breaking the diapause are unknown.

First-instar larvae have a high initial mortality, and many eggs never hatch. After larvae start feeding, though, provided food depletion and overcrowding are prevented, mortality is minimal and they usually develop rapidly. For example, *T. (Yamatotipula) tricolor* completed a generation in 69 days in the laboratory.

As larvae reach maturity, it is important to watch for inactive larvae or teneral pupae. As noted by Byers (1961) for the tipuline genus *Dolichopeza,* larvae prior to pupation are contracted and inactive. As the pupal molt becomes imminent, the larval head is deflected ventrally and pupal structures become visible through the larval cuticle. Most aquatic larvae leave the water to pupate in drier soil; most pupae immersed in water quickly die. Some species have an obligate, fourth-instar, larval diapause in which they remain contracted and inactive during the summer. I have observed this prepupal diapause in certain species of *Yamatotipula* (e.g., *T. sayi*), all reared species of *Platytipula* and *T. (Nippotipula) abdominalis*.

The best association of immature and adult stages of a species is from the last larval skin, pupal skin and emerged adult of a single individual. All the morphological characters that are needed for identification can be located on the shed skins and there is little likelihood of an erroneous association. The last larval skin is usually found near the posterior end of the pupa and may be crumpled into a compact mass. If found within one or two days after pupation (pupa will still be white or light brown), the skin can be easily stretched and cleaned in water. If the skin does not tear easily when stretched or is known to have been recently shed, I place it in water in an ultrasonic cleaning appliance and vibrate it for 10-15 seconds. The cleaned skin is then quickly restretched and stored in 70-80 percent alcohol to which a small amount of glycerin has been added.

Soon after the first pupae are found, I preserve some of the remaining larvae. Chiswell (1956) and Brindle (1960c) recommend preserving larvae in Pampel's fluid, but I have found that it is satisfactory to kill larvae by pouring water near the boiling point on them, then transferring them to storage in alcohol. This heat treatment is necessary for the expansion of the spiracular disc. Killing larvae in alcohol is unsatisfactory and results in shrunken, contracted specimens. I rarely preserve larvae in the field but, when necessary, Kahle's solution gives reasonably good specimens. Before storage in alcohol, killed larvae should be placed in the ultrasonic cleaning appliance for 10-15 seconds to remove fine dirt particles.

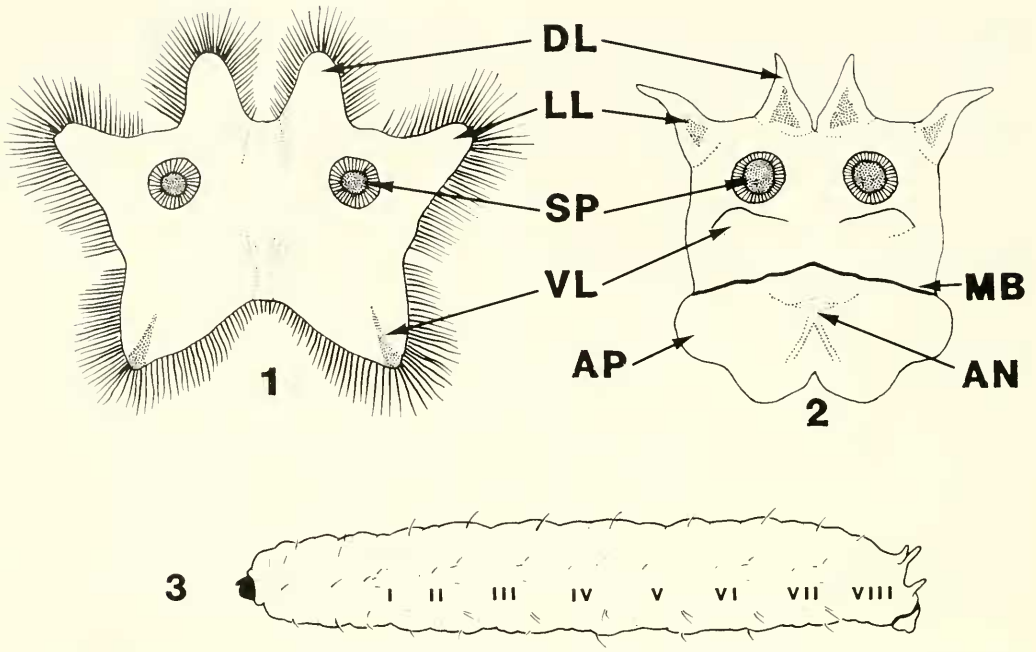
Pupae should usually be isolated from larvae, particularly if the rearing container is crowded. Pupae are delicate and should be handled as little as is possible. They can be transferred to a layer of fine damp sand or soil in a large vial with a loose fitting cap. The emerging adult needs a vertical space at least twice the length of the pupa to develop and expand properly. Once the adult has emerged, the pupal skin can be soaked for 5-10 minutes in water, then washed in a stream of water or placed in the ultrasonic vibrator. Unlike the debris on a larva or larval skin, dirt on a pupal skin is difficult to remove completely.

Morphology

Larvae of *Tipula* are elongate and cylindrical, tapering slightly at the cephalic end (Fig. 3). Mature larvae range from 12 to 60 mm in length. The black head is only partially visible, as the larval skin is attached near the anterior end of the head. The posterior end of the larva has short to long lobes surrounding two conspicuous spiracles. Beneath this spiracular area are often whitish lobes, varying in number and length, surrounding the anus. The body varies from white to brown, occasionally having a pinkish tint. Tufts of hairs and dark setae may also be seen, or the larva may appear completely hairy. Sometimes there are patterns of longitudinal lines or spots on the abdomen.

The head varies slightly from group to group, and the characters that vary are not well-suited for identification purposes. It is not described for any of the taxa treated here. A treatment of the head and its parts is found in Chiswell (1955) for *Tipula* and in Byers (1961) for a related genus, *Dolichopeza*.

Three thoracic and eight abdominal segments are clearly visible, although there are actually ten abdominal segments, according to Byers (1961). The obvious segments can be recognized by the transverse row of setae found on each segment, dorsally and ventrally. The prothoracic segment has two rows of dorsal setae, but this does not indicate two segments (Byers,



Figs. 1-3. General morphology of *Tipula* larvae. 1, spiracular area, aquatic larva. 2, spiracular area, terrestrial larva; AN-anus, AP-anal papilla, DL-dorsal lobe, LL-lateral lobe, MB-marginal band, SP-spiracle, VL-ventral lobe. 3, *T. stonei*, lateral aspect, abdominal segments I-VIII labelled; length 18 mm.

1961:734). Abdominal segment IX contains the spiracles and the immediately surrounding region. The anus and the perianal region constitute abdominal segment X, as in the adult. Abdominal segments I-VIII each appears subdivided, with a large, anterior portion (annulus) and a narrow, posterior section containing the dorsal and ventral macrosetae (Figs. 3, 16).

The cuticle is tough, hence the common name, "leather-jackets." Strong sclerotization is almost always restricted to the lobes surrounding the spiracles; the one exception is in the *T. (Lunatipula) disjuncta* group, in which dark sclerites extend from the lobes onto the dorsum of abdominal segment VIII (Fig. 56). The cuticle itself is light brown; any darker regions are caused by concentrations of hairs.

Chiswell (1956) was the first to treat the macrosetae in detail. He illustrated setal arrangements for various genera of Tipulinae and consistently applied a numbering system for the setae which I have adopted here; the homologues can be traced from genus to genus.

When specimens are roughly handled, the macrosetae can be broken off. Although the positions of broken setae can be determined from the basal sockets, information concerning setal length, thickness, and color is lost. Breakage is a primary reason for concentrating on abdominal setal arrangements; thoracic arrangements are found on only three segments, with the same arrangement repeated on the mesothorax and metathorax. In contrast, abdominal arrangements are repeated on the first seven abdominal segments, so that breakage is less of a problem.

Macrosetae of aquatic larvae are long, thin, light to dark brown (Fig. 9), and may be obscured by dense hairs. Certain aquatic groups possess setae that are branched (setae D6, L3, V1), with the distal halves of these setae divided into two to four branches (Figs. 9, 66). Branched setae have not been noted or illustrated by other authors, although groups in which the setae occur have been described.

Macrosetae of terrestrial larvae are almost always short, thick and dark brown to black (Fig. 81). Larvae of the *T. (Lunatipula) disjuncta* group and of subgenus *Odonatisca* are notable exceptions as the setae are elongate and yellow (Fig. 53). Because of the lack of long hairs on terrestrial larvae, the macrosetae are not usually obscured by hairs.

The arrangement of setae often differs be-

tween groups, but seems to be constant within a group (or, at least, within a particular species). Three sets of setae are present on each abdominal segment: dorsal, ventral and pleural. The dorsal and ventral setal arrangements are bilaterally symmetrical. Generally, there are six pairs of dorsal setae in two rows (Fig. 4a), five pairs of ventral setae in two rows (Fig. 4b), and four pleural setae (Fig. 4c). Seta L3 is below seta L2 and seta L1 is most often behind seta L2, but in *Nobilotipula* and the palearctic *T. (Platytipula) melanoceros* these three setae are in vertical alignment (Fig. 67).

Most aquatic or semiaquatic larvae possess the full complement of setae, but reduction in setal size, or complete absence of certain setae, is frequently seen in terrestrial larvae (e.g., Figs. 37, 54). Setae D4, D5, L1, L3, V1 and V5 are often considerably shortened and setae D5 and V1 are occasionally absent.

In addition to macrosetae, larvae of *Tipula* exhibit various kinds, sizes and patterns of finer hairs. Hairs are found on every segment except part of abdominal segment IX and most of segment X. The thoracic segments are usually covered by rather uniform, appressed silky hairs which provide no useful characters. On the other hand, hairs on abdominal segments I-VII exhibit much variation between groups and have been used in this study. On segment VIII and on the spiracular lobes they are usually long and uniform; hairs on the pleura are scattered and usually very short.

The hairs can be separated into three groups: macroscopic hairs, long microscopic hairs and short microscopic hairs. An idea of their sizes in relationship to each other and to macrosetae can be obtained from Figs. 105 and 147. In almost all larvae, the hairs are cylindrical and narrow, without longitudinal ridges, and usually dull brown (Fig. 8). In *Nobilotipula,* however, they are flattened, relatively broad, with longitudinal ridges and are reflective (Figs. 70, 71).

Macroscopic hairs are easily seen under low magnification and often equal or exceed the length of the macrosetae. They can be distinguished from setae because hairs lack the distinctive basal sockets. Although usually single, macroscopic hairs are sometimes organized into clusters or tufts. Hair clusters are made up of many hairs and surround setae D4, D5 and V2 (Fig. 147). They also may be found on abdominal dorsum VIII of *Yamatotipula* and other groups (Fig. 151) or on the apices of the spiracular and accessory lobes of *Nippotipula* (Fig. 60). They also form distinctive abdominal patterns in certain species of *Yamatotipula* (e.g., *pruinosa,* see Chiswell, 1956). Hair tufts are found only in the subgenus *Tipula* and are made up of a few, closely set dark hairs located near setae D5 and V2 but not surrounding them (Figs. 116, 117). The predominance of macroscopic hairs varies with the group but they are usually abundant only in aquatic larvae. For example, larvae of the subgenus *Angarotipula* and the *T. (Trichotipula) oropezoides* group are covered almost exclusively with these hairs (Figs. 8, 124). In *Schummelia,* they form a semicircular band on the dorsum of abdominal segment VIII (Fig. 98).

Short microscopic hairs are always organized into groups, usually short to long, transverse

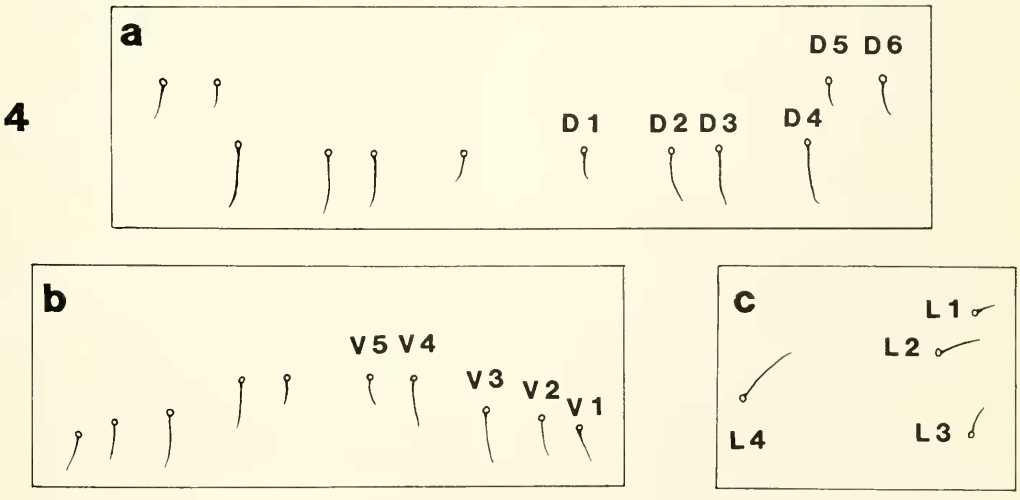


Fig. 4. Abdominal macrosetal arrangements. a, dorsal setae. b, ventral setae. c, pleural (=lateral) setae.

rows (Figs. 40, 47), and individual hairs may be difficult to discern at lower magnifications. In most terrestrial subgenera, such as *Lunatipula* or *Pterelachisus,* the body is almost exclusively covered with these hairs; a similar condition is found in the aquatic subgenera *Nippotipula, Sinotipula* and *Arctotipula.* Short microscopic hairs are entirely absent in *Tipula (Trichotipula) stonei* and the subgenus *Schummelia.* Light and dark short hairs sometimes form contrasting patterns, e.g., a spotted pattern in *T. (Yamatotipula) caloptera* (Fig. 150), dark longitudinal lines in *T. (Y.) strepens* (Fig. 151) and irregular designs in *Sinotipula* (Fig. 111) and certain species of *Savtshenkia.*

Long microscopic hairs vary in length; usually they are much shorter than macroscopic hairs but sometimes are intermediate between macroscopic and short microscopic hairs. These long hairs are always single, unlike the short hairs, and are not found in most subgenera. All three classes of hairs occur together in *T. (Yamatotipula) strepens* (Fig. 147), but long microscopic hairs predominate in *Schummelia* (Fig. 96) and *T. (Trichotipula) stonei* (Fig. 126).

The abdomen often has cuticular outgrowths that are useful for differentiating certain groups. In *Arctotipula,* abdominal segments II-VII each possess two pairs of lateral tubercles and one ventral tubercle, all of a similar conical shape (Figs. 15, 16). *Nippotipula* has one or two pairs of elongate tubercles on abdominal segment VIII and two pairs of prominent outgrowths, which I call accessory lobes, anterior to the normal six spiracular lobes (Figs. 60, 62). One species of *Savtshenkia* (unreared) has many small tubercles on the dorsum and pleura, each with a small group of hairs at its apex (Fig. 91); possibly these function to anchor the larva among aquatic mosses in the fast-flowing streams where it is found. There is a pair of small, lateral swellings in *Schummelia* on segment VIII under the band of hairs (Fig. 99).

In the subgenera *Nippotipula* and *Sinotipula* and *T. (Yamatotipula) caloptera,* transverse cuticular swellings are found on abdominal segments II-VII (Figs. 62, 108). These might be termed "creeping welts," although the swellings in *Tipula* lack recurved hooks or spinules such as those found on creeping welts of other genera (e.g., *Limonia*). They do appear to have some type of anchoring function in *Tipula,* as all three groups live in flowing water where a cuticular swelling acting as a wedge between rocks, leaf debris or mosses might maintain the larva's position against the current.

Taxonomically, the most important part is the spiracular region. This consists of the spiracular disc (segment IX, including the two prominent spiracles and the surrounding area) and the six spiracular lobes arising from the posterior border of segment VIII. Some controversy has arisen concerning which segment bears the spiracles. For example, Teskey (1981) claimed the spiracles are on segment VIII, as did Alexander (1920) and others. I agree with the view of Byers (1961) that the spiracles are on a small segment IX, part of which is later invaginated inside (forming the "spiracular yoke") during the pupal stage.

The spiracular lobes show great variation in size, structure and sclerotization but are constant in number and general position. The lobes are paired: two dorsal lobes, two lateral lobes (although they are often slightly dorsolateral) and two ventral lobes (Figs. 1, 2). In aquatic and some semiaquatic larvae, the spiracular lobes are all similar in shape and generally in size. They close against one another and around but not against the spiracles. In terrestrial larvae, the dorsal and lateral lobes are usually similar in shape, and sometimes size, but the ventral lobes are often smaller and different in shape than the other lobes. When closed, the ventral lobes, at most, are appressed against the spiracles, not against the other lobes. In aquatic species the ventral lobes are directed ventrally or posteriorly (i.e., sclerotized region facing posteriorly or dorsally, Fig. 1), whereas the ventral lobes in terrestrial species are directed dorsally (i.e., inner sclerotized region facing nearly anteriorly, Fig. 2).

Aquatic species have a glabrous region on the posterior surface of the spiracular disc that extends to the apices of the spiracular lobes. This area may be lightly to heavily sclerotized, with virtually no darkened pattern in *Sinotipula* (Fig. 110), to a distinct pattern in *Angarotipula* (Fig. 5). Many aquatic species have a dark median line on each ventral lobe and often dark, marginal bands on every lobe (Fig. 145). Terrestrial species always have the inner surface of the ventral lobes glabrous and often patterned but without dark, median lines. The dorsal and lateral lobes vary from nearly unsclerotized in the *T. (Trichotipula) stonei* group or *Pterelachisus* (Fig. 84), to having large sclerites present but some areas unsclerotized in *Serratipula* (Fig. 100), and to sclerotization of the entire posterior surfaces, forming acute points at the apices in *Lunatipula, Vestiplex* and *Odonatisca* (Figs. 41, 72, 140). Two taxa, *Nippotipula* and *Arctotipula,* appear anomalous in that they are aquatic but have the posterior surfaces of all the lobes and the spiracular disc generally unsclerotized and covered with short hairs (Fig. 14). The aquatic

and semiaquatic species nearly always possess a border of apparently hydrophobic setae around the outer margins of all spiracular lobes. In *Angarotipula,* these hairs are long and dense (Fig. 5); in *Yamatotipula,* they are shorter (Fig. 145), and in some palearctic species of *Savtshenkia* the hairs are very short. In *Beringotipula,* the short hairs encircle only the spiracular disc but do not border the lobes (Fig. 27). The border of setae is absent in fully terrestrial larvae.

A number of functions have been attributed to the spiracular lobes, although none has been investigated in detail. The similarly-shaped lobes of aquatic species, with the well-developed border of hydrophobic setae, appear suited for closing around the spiracles and trapping an air bubble. The air bubble may serve to prevent the entrance of water into the spiracles (Theowald, 1957), or may act as a physical gill (Teskey, 1981;Pritchard, 1983). Glabrous spiracular lobes with well-developed hydrophobic setae, when opened at the water surface, can keep a larva afloat, particularly if it is a small larva in the second or third instar. Brindle (1960c) disagrees with the view that the enclosed air bubble might prevent the entrance of water into the spiracles, but suggests that in semiaquatic habitats soil would be excluded.

In terrestrial larvae, only the ventral lobes are closed against the spiracles, apparently preventing the entrance of water or soil particles into the spiracles. The heavily sclerotized dorsal and lateral lobes of *Lunatipula, Odonatisca* and others probably function in locomotion; the sclerotized, pointed apices might be thrust against soil and debris (i.e., when the lobes are slightly contracted posteriorly) and serve as a brace, allowing the larva to extend its forward region.

The unsclerotized lobes of *Arctotipula* and *Nippotipula* appear to have a quite different use according to Pritchard and Stewart (1982). They found the spiracles of these aquatic taxa to be non-functional with the spiracular lobes serving as a site for cutaneous respiration. This may also be a function for the various abdominal swellings and accessory lobes of both these taxa.

The spiracles vary in size, shape and color. Nearly all groups possess circular or slightly elliptical spiracles (Figs. 125, 136), but those in *Tipula (Trichotipula) oropezoides* are distinctly trilobed (Fig. 119). The spiracles are small and widely separated in *Arctotipula* and some others (Fig. 14), and quite large and close together in a number of groups, including *Platytipula* and *Bellardina* (Figs. 20, 76). The spiracles have a central circular area, usually dark brown or black, and an outer brown ring with many slit-like openings (aeropyles). The spiracles of *Arctotipula* and *Nippotipula* are thickened and raised slightly above the surrounding surface (Fig. 14); most other groups have spiracles which are nearly flush with the surface.

The anal segment, containing the anus, is a pale, membranous region below the spiracular lobes and disc. It is always bordered basally by a thin, brown or black line called the marginal band (Fig. 2). In one subgenus, *Vestiplex,* there is an additional band extending between the anus and the more ventral papillae (Fig. 140). The anal opening is transverse. The various lobes on this segment, called anal papillae, are taxonomically important. They vary in number, placement and size and are completely absent in a few taxa. The most usual arrangement is a pair of lateral papillae and one or two pairs of median papillae (Figs. 99, 149); sometimes the median papillae are somewhat anterior to the lateral one, not strictly medial in position (Fig. 75). The size, shape and number of the papillae are distinctly correlated with habitat. They are large, elongate and/or numerous in aquatic species (Figs. 6, 90) and reduced in size and number in semiaquatic and terrestrial species (Figs. 57, 113). Brindle (1957, 1960c) discussed the specialization of the papillae and postulated an osmoregulatory function; Pritchard (1983) cited the possibility of their use in gas exchange (hence the earlier use of the term "anal gills"). The stouter medial papillae in terrestrial species are of use in locomotion, according to Chiswell (1956); they act as a pushing structure in the forward extension of the body, similar to the function postulated for hook-like dorsal and lateral lobes.

The overall morphology of *Tipula* larvae does change considerably from the first through the fourth (final) instars, and this work is based only on the morphology of the fourth-instar larva. The first-instar larva usually lacks distinct spiracular lobes, and the sclerotization of the spiracular region is rudimentary (see Hennig 1950, Fig. 205). The first instar also has a simplified macrosetal arrangement and lacks most hairs. The anal papillae may also be reduced in number from that of later instars. Second-, third- and fourth-instar larvae have spiracular regions of similar shapes, but the sclerotized patterns may change among these instars; in addition, the abdominal hairs increase in number and complexity as the larva gets older. Therefore, second and third instars may possibly be identified successfully using characters found in this work, particularly if the distinctive taxonomic features are not hair or sclerite patterns. First-instar larvae cannot be identified using the characters employed in this work.

HISTORICAL REVIEW

Much of the early taxonomic work on larvae of *Tipula* concerned only one or two species, with inadequate descriptions or illustrations. Alexander's 1920 paper remains the most relevant of these early works, for he comparatively treated the larvae of twelve species of nearctic *Tipula* and recognized the value of using a variety of characters.

J. R. Chiswell (1956) published the first major study of larval *Tipula*. Dealing with a small, local fauna (Great Britain), he was able to rear over forty percent of the species. He published complete descriptions with clear drawings and presented a key to the specific level for the fourth (final), larval instars. This study was quickly followed by a similar paper by Theowald (1957), which overlapped with Chiswell's work in some of the species treated, but additionally considered the larvae within a subgeneric classification. Theowald was the first to place the larvae of European Tipulinae in subgenera and species groupings and to discuss relationships among subgenera, based on larval characters.

In the same time period, A. Brindle published a series of smaller papers (1957-1960) describing the larvae of British *Tipula* not described previously. Brindle (1960c) gave a key to the larvae of almost 50 British species and discussed the transition of larvae from terrestrial to aquatic habitats. Savchenko (1954, 1961, 1964) also illustrated various palearctic *Tipula* larvae; in 1966 (translated into German by Theowald and Theischinger, 1979) he constructed a phylogeny for the European tipuline groups, based in part on characters of the larvae.

THE GENUS *TIPULA* LINNAEUS

A useful diagnosis for larvae of the entire genus *Tipula* cannot be constructed, as every character varies enormously within the genus, and may be found in a similar state in other tipuline genera. Only a few genera of this subfamily can be separated from all *Tipula* on the basis of characters which do not occur somewhere within *Tipula: Nephrotoma* has distinct, thickened prothoracic welts; *Leptotarsus (Longurio)* has pinnately branched anal papillae; and *Brachypremna* shows a distinct contrast between short, thoracic hairs and long, dense abdominal hairs. Yet these genera are very similar in other characters to certain larvae of *Tipula*. For example, the mostly unsclerotized spiracular area of *Nephrotoma* is similar to that of *T. (Trichotipula) stonei;* the same area of *Leptotarsus* is similar to that of *T. (Arctotipula)* and the spiracular area of *Brachypremna* suggests that of *T. (Schummelia)* and *T. (Trichotipula) oropezoides*. The remaining tipuline genera are not easily separable from *Tipula*. The similarities between larvae of the genus *Prionocera* and those of *T. (Angarotipula)* are remarkable, and the two groups can only be separated on the basis of a minor difference in hairs. A similar case exists with the genus *Holorusia* and the subgenera *Platytipula* and *Bellardina*.

Larvae remain unknown for approximately one-fourth of the nearctic subgenera of *Tipula;* these subgenera are *Eremotipula, Eumicrotipula, Labiotipula, Lindnerina, Nesotipula, Setitipula* and *Tipulodinodes*. Nearly half of the nearctic subgenera have had the larvae of only one or two of their included species reared and associated. Therefore, it seems premature to offer subgeneric descriptions now, and instead I describe one or more species within each group, and discuss the characters of the subgenus based on all known larvae.

The following key to the subgenera of *Tipula* should be used in conjunction with the generic key by Alexander and Byers (1981). Larvae of *Tipula* will key to couplets 9 and 14 in the generic key; they can then be further separated to the subgeneric level using the key presented here. Larvae of the genera *Prionocera* and *Holorusia* cannot be reliably separated from those of *Tipula* in Alexander and Byers (1981) and are therefore included in the subgeneric key for *Tipula*. Distributions given in the key refer to the entire subgenus, not individual species or species groups. The key is designed for identifying fourth-instar larvae only.

KEY TO THE SUBGENERA OF *TIPULA* AND SIMILAR GENERA

1. Usually six to eight anal papillae (Figs. 90, 149), occasionally four (Figs. 99, 123), all papillae with distinctly narrowing apices; spi-

racular lobes with developed border of setae (exceptions: *Nippotipula, Arctotipula,* Figs. 14, 60); all spiracular lobes usually similar in size and shape (Figs. 89, 145); lateral lobes equal to or smaller than ventral lobes (Figs. 5, 68, 119); when closed, all lobes are against one another; in aquatic or semiaquatic situations 2

____ Four or fewer distinct papillae (Figs. 27, 57, 140), median and often lateral papillae reduced to broad protuberances; spiracular lobes without border of setae (exceptions: *Tipula* s. str., *Savtshenkia,* in part, Fig. 113); dorsal and lateral lobes usually not similar in size and shape to ventral lobes (Figs. 84, 136); ventral lobes close against spiracles, but not against dorsal and lateral lobes; in semiaquatic to terrestrial situations 15

2(1) Border of setae around spiracular lobes reduced or absent (Figs. 14, 60); posterior surfaces of spiracular lobes with little sclerotization and covered with short microscopic hairs (Fig. 61). 3

____ Border of setae around spiracular lobes strongly developed (Figs. 5, 145); posterior surfaces of spiracular lobes sclerotized and glabrous 4

3(2) Transverse swellings on dorsum and venter of each abdominal segment I-VII (Fig. 62); two pairs of accessory lobes in addition to usual six spiracular lobes (Fig. 60); all spiracular and accessory lobes (except dorsal) with at least bifurcate apices; spiracular lobes with reduced border of setae; eastern and central North America . . . . . *Nippotipula*

____ Conical swellings, one ventral and two lateral (Figs. 15, 16) on each abdominal segment II-VII (reduced or absent in some species); accessory lobes and border of setae absent from spiracular area (Fig. 14); spiracular lobes with simple apices; northern North America . . . . . *Arctotipula*

4(2) Abdominal segment VIII with dorsal semicircular row of macroscopic hairs and pair of broad lateral swellings (Figs. 98, 99); posterior surface of each dorsal lobe with extensive dark sclerite (Fig. 93); four, short anal papillae; widespread . . . . . *Schummelia*

____ Abdominal segment VIII without row of hairs; dorsal lobes with usually only light brown sclerites; usually six to eight anal papillae . . 5

5(4) Abdominal segment II-VII each with transverse ventral swelling, width often twice height (Fig. 108); abdominal dorsum with light and dark patches of short microscopic hairs, the lighter hairs forming a pair of pale, longitudinal, marginal lines or an "H"-shaped pattern (Fig. 111); macroscopic hairs absent; spiracles separated by more than 1.5× diameter of a spiracle (usually twice or more); spiracular lobes mostly unmarked (Fig. 110); western North America. . . . . *Sinotipula*

____ No conspicuous transverse abdominal swellings (exception: *T. (Yamatotipula) caloptera,* with swellings, length 3× height, Fig. 150); abdominal dorsum usually unpatterned or, if pattern present (Figs. 150, 151), then not as above and macroscopic hairs present; spiracles separated by less than 1.5× diameter of a spiracle; spiracular lobes usually distinctly marked (Fig. 76, 119) 6

6(5) Spiracular lobes each 2-3× as long as basal widths (Fig. 5) 7

____ Spiracular lobes each less than twice as long as width at base (Figs. 68, 145). 8

7(6) Abdomen with abundant macroscopic hairs (Fig. 8) and few microscopic hairs; northern North America . . . . . *Angarotipula*

____ Abdomen with rows of short microscopic hairs (Fig. 7), macroscopic

hairs only around bases of macrosetae; northern North America . . . . . genus *Prionocera*

8(6) Four anal papillae (Fig. 123) . . 9

_____ Six or more anal papillae 10

9(8) Spiracles trilobed (Fig. 119); abdomen covered with macroscopic hairs (Fig. 124); microscopic hairs absent; widespread . . . . . . *Trichotipula,* in part *(oropezoides)*

_____ Spiracles oval or circular (Fig. 145); macroscopic hairs only in isolated clusters (Fig. 147); microscopic hairs abundant and generally distributed; widespread . . . . . *Yamatotipula,* in part *(ludoviciana)*

10(8) Eight, subequal anal papillae (Fig. 90); widespread . . . . . *Savtshenkia,* in part

_____ Six anal papillae 11

11(10) Microscopic and macroscopic hairs distinctly flattened (Fig. 70, 71), broad and reflective of light; setae L1-L3 vertically aligned (Fig. 67); eastern North America . . . . . *Nobilotipula*

_____ All hairs cylindrical and narrow (Fig. 147); pleural seta L1 posterior to seta L2 (Figs. 19, 146), setae L1-L3 not vertically aligned (exception: some species of *Platytipula*) 12

12(11) Dorsum of abdomen primarily with long and short microscopic hairs, short hairs in rows (Fig. 147); macroscopic hairs in distinct clusters around setae D4, D5, V2 (Figs. 147, 148) and on dorsum of segment VIII (anterior to separation between dorsal and lateral lobes); often a conspicuous pattern on dorsum of abdomen formed by microscopic and (rarely) macroscopic hairs (Fig. 150, 151); posterior surface of each lateral lobe with at most a faint median line (Fig. 145), setae of spiracular lobe hair border short, setal length 1/2 or less of ventral lobe width; widespread . . . . . *Yamatotipula,* in part

_____ Dorsum of abdomen primarily with macroscopic hairs, with at most indistinct clusters around setae D4 and V2 (Figs. 17, 18, 74, 79); microscopic hairs not in compact rows; no conspicuous hair patterns on abdomen; each lateral lobe usually with a dark median line, although line may be short (Figs. 20, 76); setae of spiracular lobe hair border long, setal length 3/4 or more of ventral lobe basal width. 13

13(12) Lateral and one medial pair of anal papillae curled dorsally around abdominal segment VIII (Fig. 23); abdominal setae D5 and V2 obscured by macroscopic hairs (Figs. 17, 18); each dorsal spiracular lobe sometimes with median dark line (Fig. 20) 14

_____ All anal papillae directed laterad or ventrad, not dorsad (Fig. 75); setae D5 and V2 not obscured by macroscopic hair, all setae clearly visible (Figs. 74, 79); each dorsal lobe without dark median line (Fig. 76); widespread . . . . . *Platytipula*

14(13) Dorsum of abdominal segments I-VII with microscopic hairs isolated in small patches, or scattered singly among macroscopic hairs (Fig. 24); dorsum of segment VIII without microscopic hairs (Fig. 21), western and central North America. . . . . *Bellardina*

_____ Dorsum of abdominal segments I-VII with microscopic hairs in rows intermingled with macroscopic hairs (Fig. 25); dorsum of segment VIII with microscopic and macroscopic hairs (Fig. 22); western North America . . . . . genus *Holorusia*

15(1) Border of short setae surrounding glabrous area of spiracular disc or lobes (Figs. 27, 113) 16

_____ Border of setae absent (Fig. 41) 18

16(15) Eight equally short papillae, sometimes very reduced; macroscopic hairs not in isolated clusters or tufts near setae D6 and V1; widespread

. . . . . *Savtshenkia,* in part

_____ Four papillae, lateral pair distinct lobes, ventral pair reduced to broad protuberances (Fig. 113); macroscopic hairs in clusters or tufts near setae D6 and V1 (Figs. 31, 32, 116, 117) 17

17(16) Border of short setae only around central area of spiracular disc and not on margins of the lobes (Fig. 27); each ventral spiracular lobe with finger-like, subapical projection (Figs. 28, 29); posterior surfaces of dorsal and lateral lobes without sclerotization; clusters of macroscopic hairs on dorsum and venter of abdomen (Figs. 31, 32); widespread . . . . . *Beringotipula*

_____ Border of setae extending around margins of all spiracular lobes (Fig. 113); ventral lobes without subapical projection (Fig. 115); posterior surface of each dorsal and lateral lobe mostly sclerotized; abdomen with distinct tufts of dark macroscopic hairs (Figs. 116, 117); localized in North America . . . . . *Tipula* s. str. *(paludosa)*

18(15) A dark band separating anus from anal papillae, in addition to marginal band encircling anal area (Fig. 140); setae D5 and D6 both very short, seta D6 much shorter than D1 (Fig. 143); widespread . . . . . *Vestiplex*

_____ Marginal band only (Fig. 84); seta D6 longer than D5 (Fig. 50), nearly equal to or longer than seta D1 (exception: *Pterelachisus*). . . 19

19(18) Dorsal spiracular lobes sclerotized to apices and curved cephalad (Figs. 41, 42, 56) 20

_____ Dorsal lobes without sclerotized apices, although lobes may have extensive sclerites (Figs. 48, 84) 24

20(19) Lateral spiracular lobes completely sclerotized to apices (i.e. anterior and posterior surfaces) forming long curved hooks (Figs. 57, 72) 21

_____ Posterior surface of each lateral lobe with restricted dark sclerites (Fig. 136), anterior surface unsclerotized 22

21(20) Dorsum of eighth abdominal segment with sclerites extending anteriorly from each dorsal lobe (Figs. 56, 59); widespread . . . . . *Lunatipula,* in part *(disjuncta)*

_____ Dorsum of eighth abdominal segment without sclerites (Fig. 73). (See text discussion of *Odonatisca*); widespread and northern North America, respectively . . . . . *Lunatipula,* in part; *Odonatisca*

22(20) Each ventral lobe small, narrow basally, apex truncated, 1/2 to 2/3 of lobe with dark sclerite not extending onto central spiracular surface (Figs. 35, 138, 139); ventral lobes each with a long seta at apex; short microscopic hairs dense, with bare areas ("setal imprints") extending medioposteriorly from bases of setae D1-D3 (Figs. 39, 134) . . 23

_____ Each ventral lobe triangular in posterior aspect, wide basally, apex rounded, dark sclerite of inner surface extending onto spiracular surface (Figs. 43, 45); ventral lobes each with only very short setae at apex; short microscopic hairs not dense, without "setal imprints" (Fig. 46); widespread . . . . . *Lunatipula,* in part

23(22) Seta D4 short to long and always dark; one or two dark spots at base of each ventral lobe (Fig. 139); short microscopic hairs in coalescing rows with strongly developed "setal imprints" (Fig. 134); widespread. . . . . *Triplicitipula,* in part

_____ Seta D4 pale distally and of medium length; no spots at bases of ventral lobes (Fig. 35); short microscopic hairs in small, separated groups with weakly developed "setal imprints" (Fig. 39); western North America . . . . *Hesperotipula*

24(19) Short microscopic hairs absent (Fig. 126); anal papillae without distinct lobes (Fig. 125); lateral spiracular lobes long and narrow;

ventral lobes without appreciable sclerotization (Fig. 130); widespread . . . . . *Trichotipula,* in part *(stonei)*

_____ Short microscopic hairs abundant and in short rows (Figs. 47, 86); anal papillae reduced but lateral lobes distinctly visible (Fig. 48, 100); lateral spiracular lobes not particularly narrow or long; ventral lobes with extensive sclerites (Fig. 85, 102) 25

25(24) Macroseta D6 short, much shorter than D1 (Fig. 81); seta D5 often only represented as a basal socket; sclerotization of posterior surface of each dorsal lobe not extensive, usually only on basal 1/3 of lobe (Fig. 84); widespread . . . . . *Pterelachisus*

_____ Seta D6 long, similar in length to D1 (Fig. 103); seta D5 present; sclerotization of dorsal lobes extensive, covering basal 1/2 to 2/3 of each lobe (Figs. 48, 100). 26

26(25) Each ventral lobe small, with truncate apex in lateral aspect (Figs. 136, 138); dark sclerite of each lobe not extending onto central spiracular surface; a long seta at apex of each ventral lobe; widespread . . . . *Triplicitipula,* in part *(simplex)*

_____ Each ventral lobe triangular in posterior aspect, or with rounded apex (Figs. 44, 100); dark sclerite of each lobe extending onto spiracular surface; short setae only at apex of each ventral lobe (Figs. 49, 102) 27

27(26) Sclerites of dorsal and lateral lobes light brown (Fig. 100); inner circle of each spiracle brown; seta D4 equal in length to seta D1 (Fig. 103); California, Oregon. . . . . *Serratipula*

_____ Sclerites of dorsal and lateral lobes dark brown to black (Fig. 48); inner circle of each spiracle black; seta D4 shorter than seta D1 (Fig. 50); widespread . . . . . *Lunatipula,* in part *(morrisoni)*

SUBGENERIC ACCOUNTS

Subgenus *Angarotipula* Savchenko

Of the two nearctic species of *Angarotipula,* only the larva of *Tipula illustris* has been reared and associated with adults.

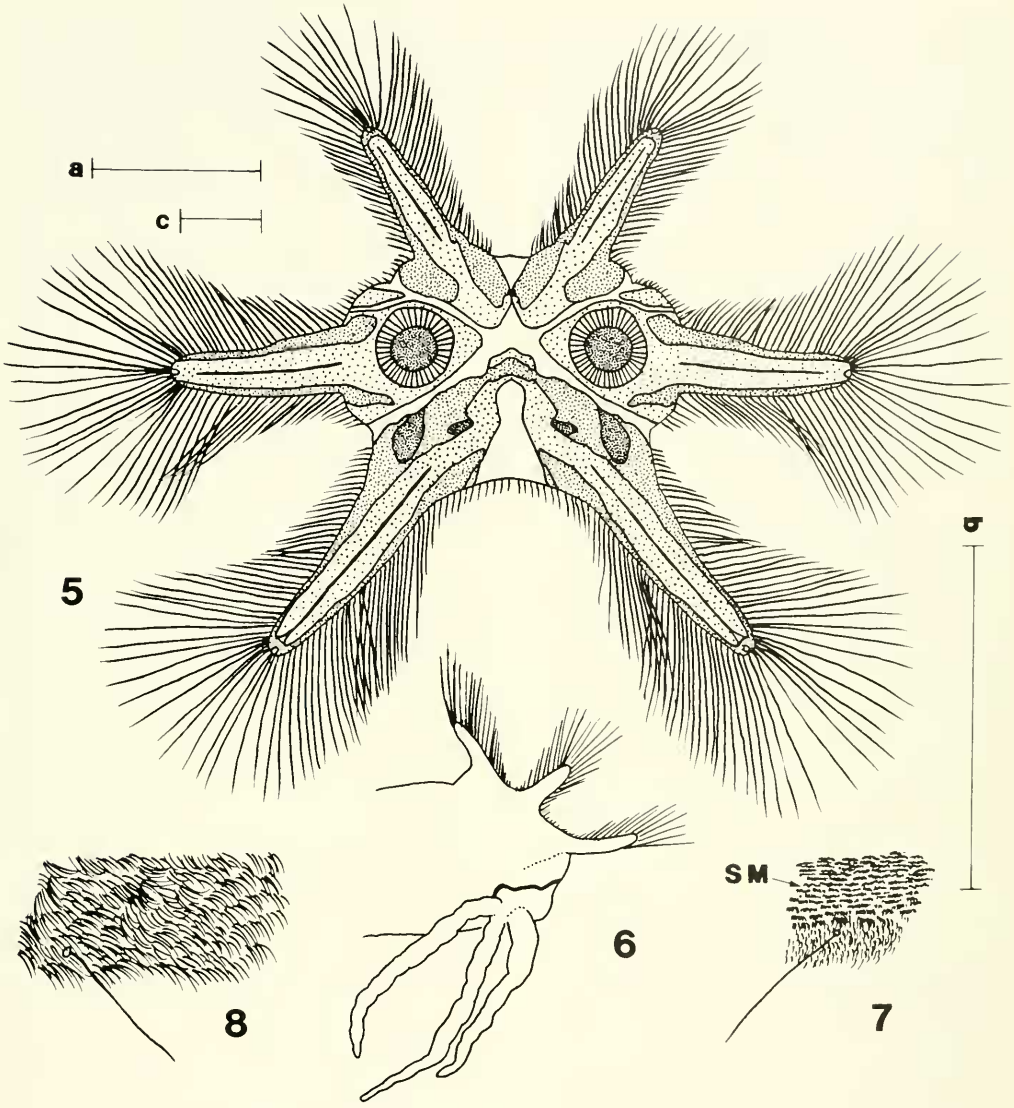
Tipula (Angarotipula) illustris Doane

Malloch 1917:199-200, figures (as *Tipula* sp. 1).
Alexander 1920:996-997, Figs. 498-502 (as *Prionocera fuscipennis*).

DESCRIPTION: Length 20.0-24.7 mm, width 2.6-3.1 mm, body yellowish brown. *Abdomen:* Macrosetae brown, setae D1-D4 long, D5 and D6 slightly shorter, D6 branched (Fig. 9). Setae L1, L2 and L4 long, L3 shorter and branched (Fig. 10). Setae V2-V4 long, V1 and V5 slightly shorter, V1 branched (Fig. 11). Macroscopic hairs abundant, densest on dorsum (Fig. 8), short microscopic hairs only along cuticular folds on venter. *Spiracular Disc:* All spiracular lobes long and narrow, each at least 3× as long as width at base, ventral lobes often 4× as long as wide, lateral lobes equidistant from dorsal and ventral lobes (Fig. 5). Lateral lobes 1.25× as long as dorsal lobes, ventral lobes approximately twice as long as dorsal lobes. Lobes with well-developed border of setae, longest setae twice basal width of lobe. Posterior surface of each lobe with median dark line extending from near base to near apex of lobe; each lobe with dark, lateral sclerites from base to apex, outer sclerites of ventral lobes extending as thin band across middle of spiracular surface. Two black spots near base of each ventral lobe. Remainder of spiracular disc yellowish. Spiracles circular, black. Marginal band light brown. *Anal Segment:* Six, subequal, elongate anal papillae (Fig. 6),. lateral papillae single, medial papillae paired, length/basal width approximately 6-11.

SPECIMENS EXAMINED: Nine larvae from the following localities in ONTARIO: South March; Dunrobin; 9.7 km W of Richmond; Galt; all collected by H. Teskey (CNC).

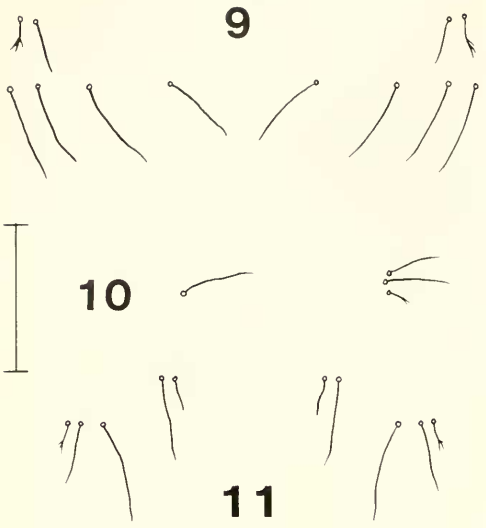
SUBGENERIC DISCUSSION: The most distinctive feature of *Angarotipula* is the long, narrow spiracular lobes, each approximately three times its basal width. Each lobe has a complete border of long setae and a dark, median line extending the length of the lobe. The sclerotized pattern on the spiracular disc is quite recognizable, particularly the dark band extending across the middle of the disc from the outer lateral areas of each ventral lobe. The body is covered by macroscopic hairs; short micro-



Figs. 5, 6, 8. *Tipula (Angarotipula) illustris.* 5, spiracular area. 6, terminal abdominal segments, lateral aspect. 8, example of abdominal macroscopic hairs. Fig. 7. *Prionocera dimidiata,* example of abdominal microscopic hairs; SM-short microscopic hairs. All scale lines 1 mm. Scale a: Fig. 5, scale b: Figs. 7, 8, scale c: Fig. 6.

scopic hairs are only along the cuticular folds.

Larvae of *Angarotipula* are more similar to those of the genus *Prionocera* than to any other larvae of *Tipula.* In fact, the two groups have proven difficult to separate as larvae, for only minor structural differences exist and they may occur in similar habitats. The most important similarities between *Angarotipula* and *Prionocera* are the long, narrow spiracular lobes, virtually identical pattern of sclerotization on the spiracular disc including a dark, median line on each lobe, a well-developed border of setae, six elongate anal papillae, and a similar arrangement of abdominal macrosetae. One feature separates the two groups: in *Angarotipula,* there is a predomi-



Figs. 9-11. *Tipula (Angarotipula) illustris,* abdominal macrosetae. 9, dorsal setae. 10, pleural setae. 11, ventral setae. Scale line 1 mm.

nance of macroscopic hairs on the abdomen, with short microscopic hairs virtually absent (Fig. 8); by contrast, the abdomen of *Prionocera* is covered with rows of short microscopic hairs with macroscopic hairs only around the bases of the dorsal and ventral macrosetae (Fig. 7).

HABITATS OF *ANGAROTIPULA:* The larval habitat of *Tipula illustris* was first described by Malloch (1917, as *Tipula* sp. no. 1) as "in an inlet among weeds at the surface." Alexander (1920, as *Prionocera fuscipennis*) collected *T. illustris* larvae in New York from a cattail swamp and also found pupal skins among *Sparganium* stems. Rogers (1942, as *Prionocera fuscipennis*) collected larvae in Michigan from "sodden, partially or wholly submerged plant detritus of the marshes and seepage areas." He found them particularly characteristic of leaf-filled or vegetation-choked channels or pools. Teskey (collection labels, CNC) found *T. illustris* larvae in Ontario in the saturated grassy soil margin of a small pool and also in a rotten log in a swamp.

G. W. Byers (collection label, KU) collected pupae of *T. parrioides* in Alaska from the margin of a pond.

Subgenus *Arctotipula* Alexander

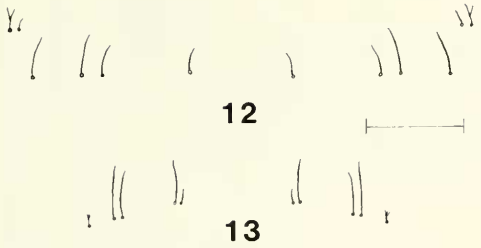
Of the 21 nearctic species of *Arctotipula,* only *Tipula sacra* is known from reared larvae associated with adults.

Tipula (Arctotipula) sacra Alexander

Pritchard and Hall 1971:474-477, Figs. 8-12, 22.

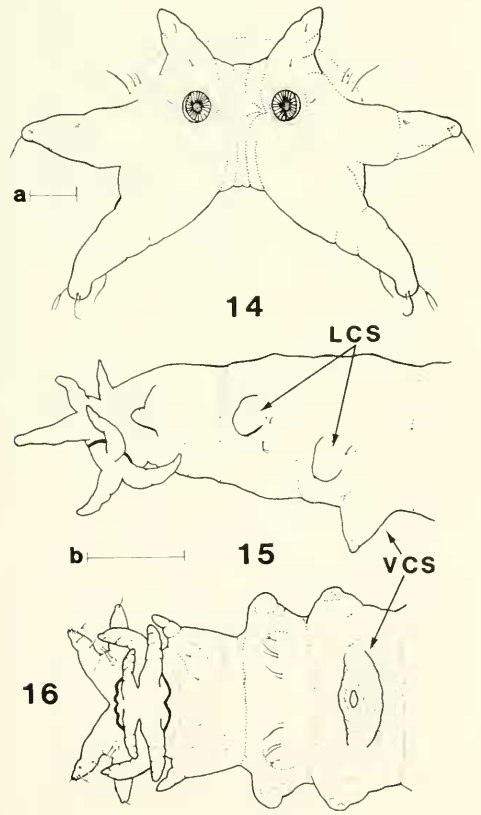
DESCRIPTION: Length 28.6-42.9 mm, width 3.9-5.1 mm, body light brown, slightly dorsoventrally depressed. *Abdomen:* Three pairs of conspicuous conical tubercles on segments II-VII, increasing in size posteriorly, largest tubercle twice as wide as long. Two pairs of tubercles on each pleural segment, one pair medioanteriorly, one pair dorsoposteriorly; third pair medioanteriorly on venter (Fig. 15). An additional pair of lateral tubercles on segment VIII, anterior to lateral spiracular lobes (Fig. 16). Macrosetae light brown. Setae D1, D5 and D6 short, D2-D4 longer, D6 usually branched (Fig. 12). Seta L1 short, L2-L4 longer, L3 usually branched. Setae V5 and V1 short, V2-V4 longer, V1 branched (Fig. 13). Short microscopic hairs covering abdomen, in transverse rows on dorsum and venter, single on pleura. An irregular pattern of lighter, circular areas sometimes visible on dorsum, pattern due to sparse microscopic hairs within the circular areas. Long microscopic and macroscopic hairs absent. *Spiracular Disc:* All spiracular lobes conical, dorsal lobe shortest, slightly longer than width at base, length of lateral lobe 1.5× length of dorsal lobe, length of ventral lobe 2.5× length of dorsal lobe (Fig. 14). Lateral lobes approximately equidistant from dorsal and ventral lobes. Lobes without darker sclerites. Spiracular disc and lobes completely covered with single short microscopic hairs except area surrounding spiracles. Macrosetae on posterior surface of all lobes; two macrosetae on dorsal lobe, near base and $^2/_3$ lobe length; on lateral lobe, one to three at midlength, two at tip; two setae at tip of ventral lobe. Spiracles small, circular and widely separated by at least twice diameter of spiracle; inner circle dark, outer ring brown, spiracles noticeably raised from cuticular surface. Marginal band brown. *Anal Segment:* Six elongate anal papillae (Fig. 16), medial papillae paired, lateral papillae single, length/basal width 3-5.

SPECIMENS EXAMINED: Thirty-three larvae from the following localities in ALBERTA: Kananaskis Valley, Lusk Creek, H. Teskey, coll. (CNC); same locality as preceding, G. Pritchard, coll. (GP,JKG); Maycroft, H. Teskey, coll. (CNC).



Figs. 12, 13. *Tipula (Arctotipula) sacra,* abdominal macrosetae. 12, dorsal setae. 13, ventral setae. Scale line 1 mm.

Subgeneric Discussion: Larvae of *Arctotipula,* based on *Tipula sacra* and the palearctic *T. salicetorum,* share a number of unique features. Both species possess conical, unsclerotized spiracular lobes which are almost completely covered with short microscopic hairs, and the dorsal lobes are noticeably shorter than the lateral and ventral lobes. Very striking is the absence of a developed border of setae around the spiracular lobes. Both species have small, widely separated spiracles, six long anal papillae, and the spiracular lobes may be tipped with clusters of macroscopic hairs (in *T. salicetorum*). Also notable are the presence of three pairs of cuticular swellings on abdominal segments 2-7, and an additional pair of swellings on segment 8. The body is slightly depressed, macrosetal patterns are similar in both species, short microscopic hairs predominate and there are almost no macroscopic hairs.



Figs. 14-16. *Tipula (Arctotipula) sacra.* 14, spiracular area. 15, terminal abdominal segments, lateral aspect, segments VII-X. 16, same segments as 15, ventral aspect; LCS-lateral conical swelling, VCS-ventral conical swelling. All scale lines 1 mm. Scale a: Figs. 15, 16, scale b: Fig. 14.

Certain unreared larvae, undoubtedly *Arctotipula,* have been figured previously and deserve comment here. Although possessing the basic *Arctotipula* form, these show additional variation in certain characters. Alexander (1919) described and illustrated a probable *Arctotipula* as Tipuline no. 2. This larva has the abdominal dorsum strikingly patterned with three dark longitudinal stripes. *Tipula sacra* often has a light pattern of pale circular spots on the dorsum of the abdomen. Savchenko (1961) illustrated two types of larvae as *Tipula (?Arctotipula)* sp. no. 1 and 2. Each dorsal spiracular lobe of species no. 2 has a dark, narrow median sclerite with additional dark sclerites just below the spiracles. I have seen this pattern of sclerotization on unassociated larvae collected in Alaska. In addition, these Alaskan specimens have the abdominal tubercles only as low bumps and the anal papillae are short.

Arctotipula shows many morphological similarities to *Nippotipula* and few to other subgeneric groups. The shape of the spiracular lobes, the general lack of sclerotization on the lobes, the short microscopic hairs covering the spiracular disc and the inability to close the spiracular lobes are all characters seen only in these two subgenera. The larvae of both, although aquatic, lack the well-developed border of setae around the spiracular lobes as found in other aquatic subgenera. The presence

of distinct abdominal cuticular swellings is found in *Arctotipula, Sinotipula* and *Nippotipula,* but the conical swellings in *Arctotipula* differ in position and shape from the transverse swellings of the others. The reduction of the spiracles and the almost complete lack of macroscopic hairs are also shared by these three subgenera.

HABITATS OF *ARCTOTIPULA:* The life history of *Tipula sacra* has been detailed in an excellent series of papers by Pritchard and Hall, including a general life history (Pritchard and Hall, 1971), larval food and development (Hall and Pritchard, 1975, Pritchard, 1976) and population dynamics (Pritchard 1978,1980). Pritchard and Hall found the larvae inhabiting the bottom sediments of well-oxygenated, abandoned beaver ponds. Unreared larvae of *Arctotipula* have been found in similar situations. The specimens of "Tipuline no. 2" of Alexander (1919) were collected in Alaska from "melted ponds in the tundra." I have seen other unreared larvae collected by W. L. Jellison from a pond drain in Montana and by D. G. Huggins in Alaska from the rocky bottom of a lake, near shore.

Tipula salicetorum, although not reared from the larva to the adult, has had larvae assigned to it with certainty. Hofsvang (1979) reports the larvae as inhabiting the littoral zone of a subalpine lake in southern Norway.

Subgenus *Bellardina* Edwards

The larvae of two species in this subgenus, *Tipula pura* and *T. albimacula,* have been reared during this study.

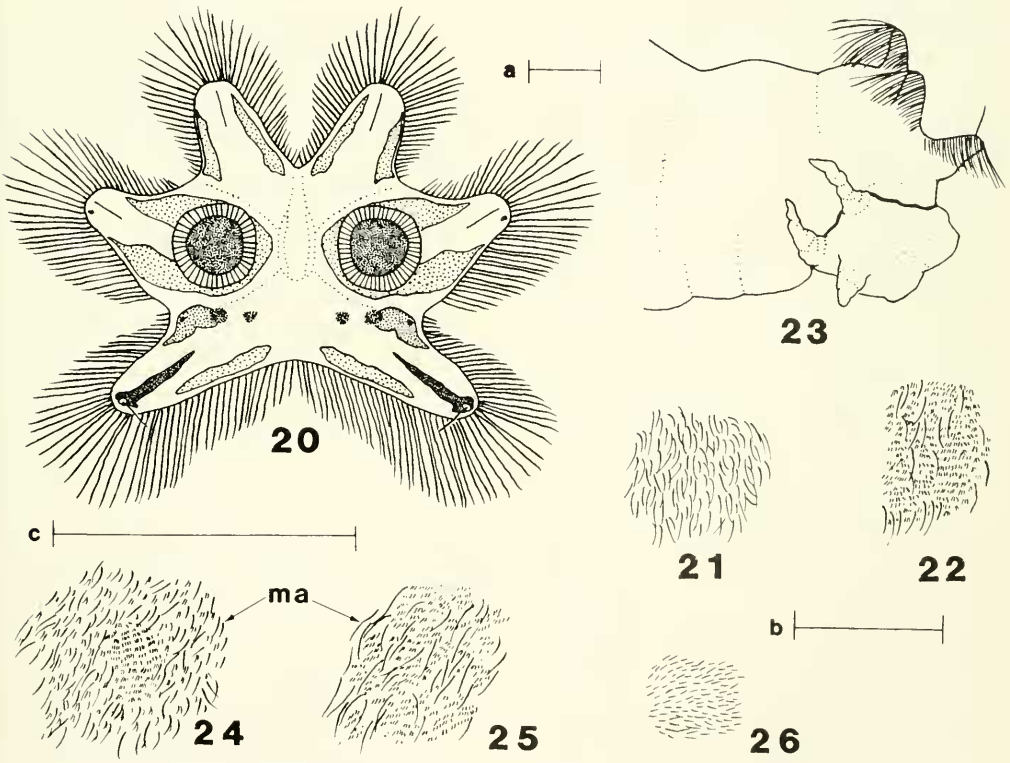
Tipula (Bellardina) pura Alexander

DESCRIPTION: Length 33.6-39.3 mm, width 4.3-5.0 mm, body light brown. *Abdomen:* Macrosetae dark brown, setae D2-D4 long, D1 and D6 shorter, D5 pale and very short, D6 branched (Fig. 17). Setae L2 and L4 long, L1 and L3 shorter, L3 branched (Fig. 19). Setae V3 long, V1, V4 and V5 shorter, V2 pale and very short, V1 often branched (Fig. 18). Scattered, single macroscopic hairs longest and more dense on dorsum of segment VIII, and around bases of setae D5 and V2 (Fig. 21); short microscopic hairs in short rows, along body folds, in paired subcircular areas on dorsum and scattered singly among macroscopic hairs (Fig. 24). Hair on pleura single (Fig. 26). *Spiracular Disc:* All lobes subequal, approximately as long as width at base, lateral lobes equidistant from dorsal and ventral lobes (Fig. 20). Lobes with a well-developed border of setae, longest setae slightly less than basal width of lobe. Posterior surface of each lobe with two light brown marginal sclerites, sclerites of lateral lobes extending around spiracles. Each ventral lobe with a dark median line, extending almost length of lobe; three dark spots at base of lobe; a long seta near apex. Dorsal and lateral lobes often with faint median line, approximately ½ length of lobe; a dark spot at apex of lateral lobe. Spiracles large, circular, inner circle dark brown, outer ring brown; distance between spiracles equal approximately to diameter of a spiracle. Remainder of spiracular disc pale. Marginal band brown. *Anal Segment:* Six anal papillae, four elongate and curled dorsad around abdomen, two short and extending ventrad (Fig. 23); length/basal width of posterior papillae 2-3, smallest papillae length/basal width 1-1.5.

SPECIMENS EXAMINED: Seventeen larvae from Gravel Pit Lakes State Recreation Area, 24.1 km W of Cimarron, on U.S. Highway 64, Colfax Co., New Mexico, J. K. Gelhaus, coll. (JKG).

SUBGENERIC DISCUSSION: *Bellardina,* to judge by *Tipula albimacula* and *T. pura,* forms a homogeneous group defined by rather generalized characters. The spiracular lobes are subequal, of medium length, and have a well-developed border of long setae. The pattern of sclerotization on the lobes is similar in both species: each ventral lobe always has a dark median line and three dark spots at the base; the dorsal and lateral lobes may also have short, faint median lines; all lobes have light brown, marginal sclerites. There are six anal papillae, four of which are elongate and curled dorsad around the abdomen. The spiracles are large, circular and not widely separated. Setae D5 and V2 are pale and difficult to see among macroscopic hairs, unlike the other, easily visible macrosetae. In fact, macroscopic hairs predominate on the body; short microscopic hairs are only restrictedly present in certain areas and are single or in short rows. Setae D6, V1 and L3 are usually branched. The larvae of both species attain a large size at maturity (30-40 mm).

Figs. 17-19. *Tipula (Bellardina) pura,* abdominal macrosetae and macroscopic hair clusters. 17, dorsal setae. 18, ventral setae. 19, pleural setae. Scale line 1 mm.



Figs. 20, 21, 23, 24, 26. *Tipula (Bellardina) pura.* 20, spiracular area. 21, example of hairs on dorsum of abdominal segment VIII. 23, terminal abdominal segments, lateral aspect. 24, example of hairs on dorsum of abdominal segments I-VII; ma-macroscopic hairs. 26, example of hairs on abdominal pleura. Figs. 22, 25. *Holorusia rubiginosa.* 22, same area as Fig. 21. 25, same area as Fig. 24. All scale lines 1 mm. Scale a: Fig. 23, scale b: Fig. 20, scale c: Figs. 21, 22, 24-26.

Many of the characters listed above are shared by other aquatic groups. For example, subequal lobes with a border of long setae, elongate anal papillae, dark median lines on the ventral lobes, abundant macroscopic hairs and branched setae are also

found in other groups such as *Yamatotipula*, *Platytipula*, the non-nearctic *Acutipula*, and the genus *Holorusia*. Consequently, separation of *Bellardina* from *Yamatotipula*, *Platytipula* and particularly *Holorusia* is rather difficult. *Yamatotipula* is distinguished by conspicuous, well-defined clusters of macroscopic hairs around setae D4, D5 and V2 and may also have conspicuous patterns of microscopic hairs; although setae D5 and V2 are obscured by macroscopic hairs in *Bellardina*, these hairs do not form distinct clusters but are simply part of the overall abundance of hairs. Additionally, short microscopic hairs are sparse and never form conspicuous patterns as seen in *Yamatotipula*.

Platytipula and *Holorusia* both have the abdomen generally covered with short microscopic hairs organized in long rows; macroscopic hairs are abundantly scattered between these rows (Figs. 22, 25). *Bellardina* has small areas of only short microscopic hairs which are not in long rows nor predominantly intermingled with macroscopic hairs (Figs. 21, 24). Other microscopic hairs are found singly among the macroscopic hairs, never in rows. The anal papillae of *Platytipula* extend laterally or ventrally and never curl upward; setae D5 and V2 are also not obscured by long hairs as in *Bellardina*. Also, the dorsal lobes may have median lines in *Bellardina* but never in *Platytipula*.

As more larvae have been associated, particularly those of *Platytipula* and *Bellardina*, the characters used in the key by Alexander and Byers (1981) for the separation of the genera *Tipula* and *Holorusia* have not proven to be useful and, consequently, have not been used in the present key.

HABITATS OF *BELLARDINA*: *Bellardina* occurs exclusively in the New World, with five species in North America. Four of the five are found only in the West; one other (*T. albimacula*) extends into the Central Plains.

Larvae of *T. pura* were found along the margins of a spring-fed, seepage-stream which ran for 15 m before its confluence with the Cimarron River, in New Mexico. Twenty mature larvae were found in a 30 cm square area in an exposed mud bank; additional larvae were collected in a nearby bank among roots of grasses and nettles.

Similar spring-fed aquatic habitats yielded larvae of *T. albimacula* at three localities in Kansas, all within the Flint Hills prairie region (Gelhaus, field notes). Larvae occurred in springs emanating from limestone outcroppings, specifically, among mats of watercress or aquatic mosses and apparently only from the upper areas of these springs; none were collected along the spring-fed streams.

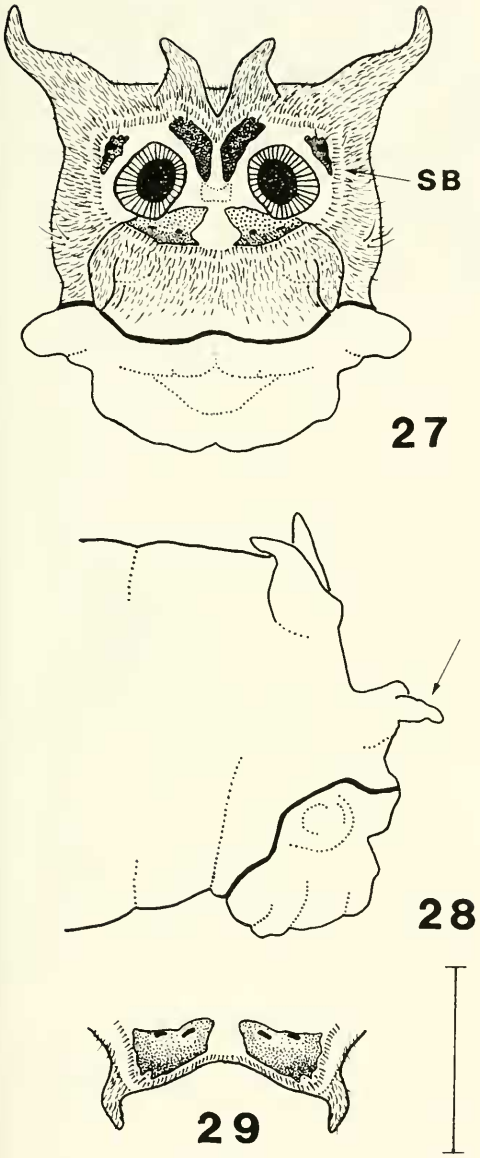
Subgenus *Beringotipula* Savchenko

I have seen larvae associated with adults for three species in this subgenus.

Tipula (Beringotipula) rohweri Doane

DESCRIPTION: Length 19.7-23.6 mm, width 2.1-2.7 mm, body light brown. *Abdomen:* Macrosetae brown, setae D2 and D3 long, D1 and D6 slightly shorter, D4 short and pale apically, D5 absent (Fig. 31). Seta L2 long, L1, L3 and L4 shorter (Fig. 30). Seta V1 long, V3-V5 slightly shorter, V2 absent (Fig. 32). Dorsum and venter with short microscopic hairs in short transverse rows, with single long microscopic hairs scattered between rows (Figs. 31, 32). Macroscopic hairs on dorsum of segments VII and VIII and in clusters near seta D6, and around D3 and D4, and V1 and V3, ventral clusters most conspicuous. Pleura with single short microscopic hairs (Fig. 30). *Spiracular Disc:* Dorsal and lateral lobes conical, lateral lobes dorsolateral, close to dorsal lobes, lateral lobes 2.0-2.5× length of dorsal lobe (Fig. 27). Lobes unsclerotized, with scattered single macroscopic hairs. A dark irregular sclerite near base of each dorsal and lateral lobe. Ventral lobes roughly triangular, as wide as long, with finger-like projection on lateral surface of lobe near apex (Fig. 28), projection approximately ½ to one length of ventral lobe (Fig. 29). Inner surface of each ventral lobe with sclerite extending to spiracle, outer edge darkest; two dark spots near inner edge. Remainder of ventral lobe with single long microscopic hairs. Border of very short setae around circumference of glabrous area of spiracular disc. Spiracles roughly oval, inner circle black, outer ring dark brown. Marginal band brown. *Anal Segment:* Four, short anal papillae (Fig. 27); each lateral papilla approximately as long as wide; each ventral papilla a broad, low swelling. Anal opening transverse.

SPECIMENS EXAMINED: Seven larvae from



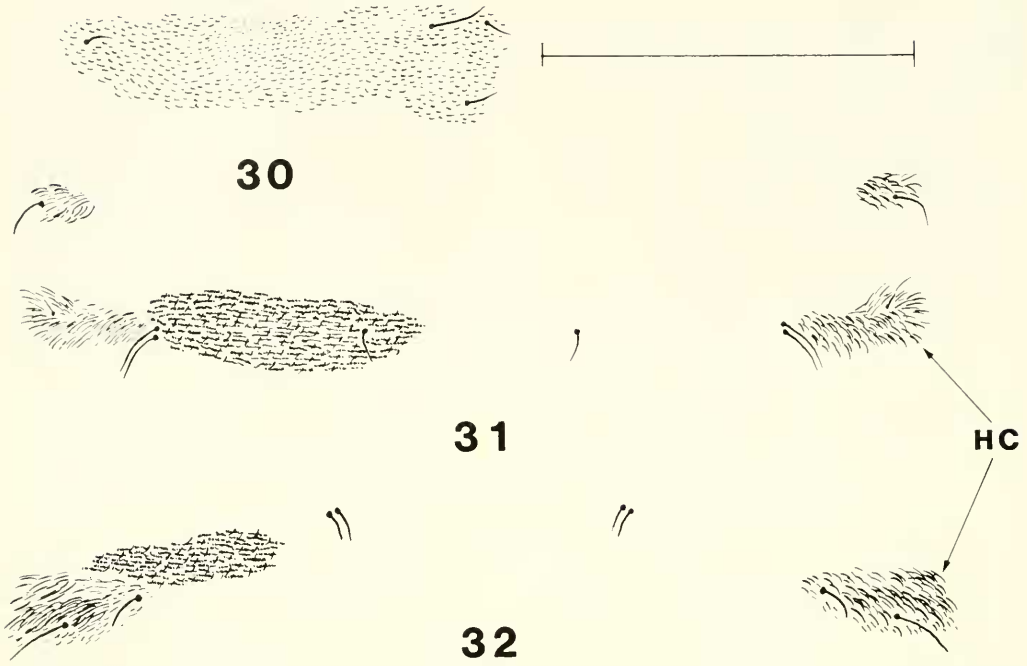
Figs. 27-29. *Tipula (Beringotipula) rohweri.* 27, spiracular area; SB-setal border. 28, terminal abdominal segments, lateral aspect. 29, ventral spiracular lobes, dorsal aspect. Scale line 1 mm.

Gravel Pit Lakes State Recreation Area, 24.1 km W of Cimarron, on U.S. Highway 64, Colfax Co., New Mexico, J. K. Gelhaus, coll. (JKG).

SUBGENERIC DISCUSSION: The larvae of *Beringotipula* form a very homogeneous group judging from the nearctic species examined, *Tipula rohweri, fallax* and *resurgens,* and the description of a palearctic species, *T. unca.* A unique feature is the digitiform projection located just below the apex of each ventral lobe. This protuberance is small (wider than long) in *T. unca* but is much longer than wide in the other known species. Wedge shaped, sclerotized spots occur near the base of each dorsal and lateral lobe but the lobes are unsclerotized and covered with single macroscopic hairs. The inner surface of each ventral lobe is sclerotized nearly to the apex and the lobes close against the spiracles. A border of short setae surrounds the glabrous area of the spiracular disc. The pattern of the darkened sclerites on the spiracular disc is similar in all the species examined. The anal papillae are short, with the lateral pair bluntly conical and the ventral papillae present only as broad protuberances. The abdomen has conspicuous, although slightly diffuse, clusters of macroscopic hairs around macrosetae V1 and V3, D3 and D4, and medial to D6. Additionally, the dorsum and venter of the abdomen has short microscopic hairs arranged in rows, with long microscopic hairs placed singly between these rows. Macroseta D4 is short and setae D5 and V2 are absent.

In the shape, size and placement of the spiracular lobes, *Beringotipula* is similar to *Pterelachisus, Savtshenkia* (cf. palearctic species *T. obsoleta* and *signata*), and the palearctic groups *Nigrotipula* and *Oreomyza.* A border of very short spiracular setae is found in the genus *Ctenophora* (cf. *C. elegans*) and the subgenera *Tipula* s. str. and *Savtshenkia* (cf. *T. signata* group sensu Theowald, 1957) as well as in *Beringotipula.* No other subgenus of *Tipula* shows a digitiform projection on each ventral lobe, but a similarity in form is found on the dorsal and lateral lobes of *Tipula* s. str. whereby each lobe is constricted distal to the sclerotized region. *Yamatotipula,* the palearctic *Acutipula* and *Beringotipula* all possess distinct macroscopic hair clusters in similar positions on the abdomen.

Beringotipula cannot be confused easily with other subgenera. The digitiform projection on each ventral lobe is unique among known tipulines, and few other taxa



Figs. 30-32. *Tipula (Beringotipula) rohweri.* 30, macrosetae and example of hairs on abdominal pleura. 31, macrosetae, hair clusters and some of the microscopic hairs, representative of abdominal dorsum I-VII; HC-hair clusters. 32, same structures as 31, ventral abdominal segments I-VII. Scale line 1 mm.

have both unsclerotized dorsal and lateral lobes and a short setal border. Although *Pterelachisus* and the palearctic *Oreomyza* and *Nigrotipula* have the spiracular disc similar to that of *Beringotipula,* they do not have the border of spiracular setae. (Correction added in proof: Theowald van Leeuwen, University of Amsterdam, informs me that a small digitiform projection on each ventral spiracular lobe is found also in larvae of the palearctic subgenus *Tipula (Mediotipula).*)

HABITATS OF *BERINGOTIPULA: Beringotipula* includes nearly 25 nearctic species whose known larvae occur in very wet habitats. Larvae of *Tipula rohweri* were collected from sodden, well-rotted logs at the edge of or lying across a small spring-fed stream in an oak-pine forest. Larvae were under the surface mosses or in the very decayed outer layers of the logs. At the same locality, other larvae of this species were found along the grassy margin of a small cold seep in the top layer of saturated soil enriched by pine needles and leaf fragments of deciduous trees.

Other species occur in similar semi-aquatic habitats. In California, I found larvae of *T. fallax* in the sandy margins of a small mountain creek, and also in mosses on a vertical limestone cliff over which water slowly trickled. In New Mexico, one larva, possibly of *T. appendiculata,* was in a leaf pack in a rapidly flowing stream.

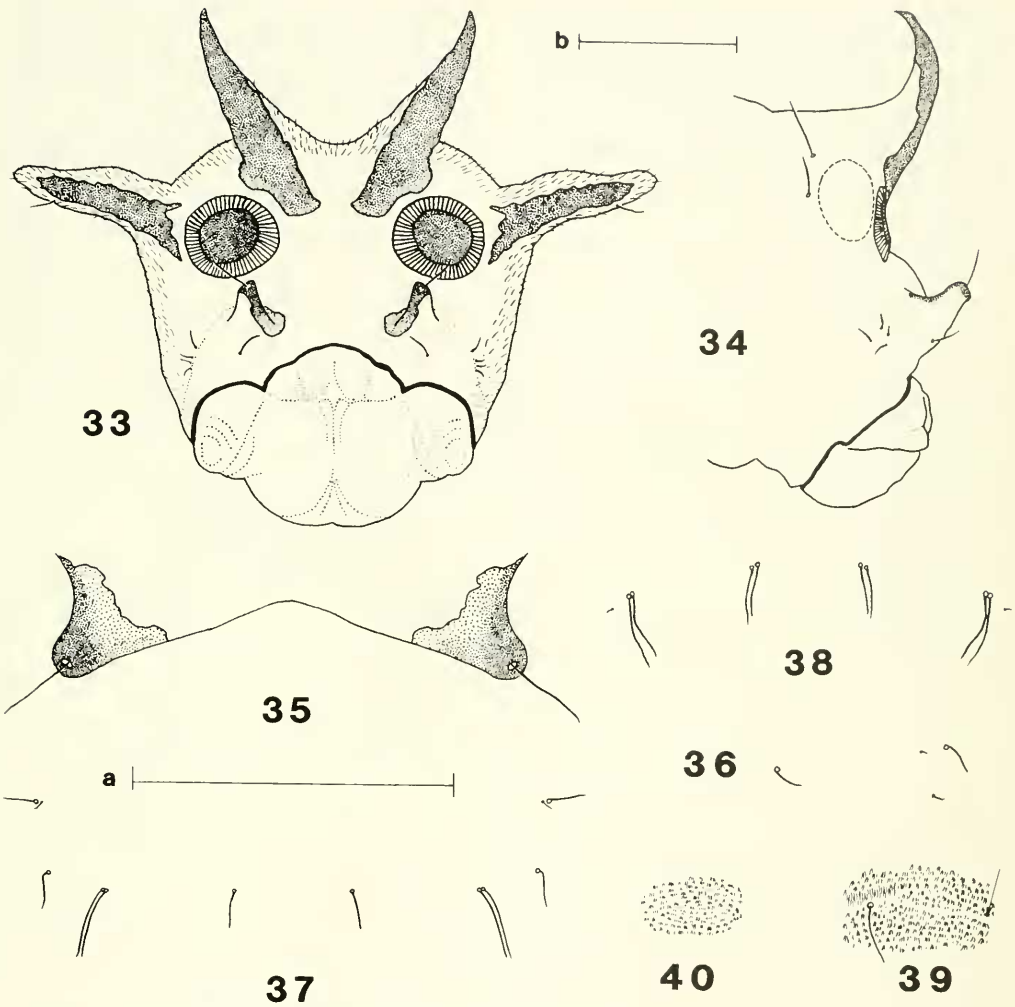
The larva of the palearctic *T. unca* has been collected from wet forest soil, often at the edges of streams and in wet moss cushions (Theowald, 1967).

Subgenus *Hesperotipula* Alexander

Of the over 20 nearctic species included in this group, the larva of only one has been reared and associated with adults.

Tipula (Hesperotipula) aitkeniana Alexander

DESCRIPTION: Length 19.2-24.3 mm, width 3.3-4.0 mm, body brownish white. *Abdomen:* All macrosetae dark brown to black, setae D2-D3 long, D1, D4 and D6 shorter, D5 very short, D4 appressed and pale distally (Fig. 37). Setae L1 and L4 long, L2 and L3 very short and appressed (Fig. 36). Setae V2-V5 long, V1 very



Figs. 33-40. *Tipula (Hesperotipula) aitkeniana.* 33, spiracular area. 34, terminal abdominal segments, lateral aspect; lateral lobe omitted. 35, ventral spiracular lobes, dorsal aspect. 36, pleural abdominal macrosetae. 37, dorsal abdominal macrosetae. 38, ventral abdominal macrosetae. 39, microscopic hairs around seta D1, showing "setal imprints". 40, example of microscopic hairs on dorsum of abdomen. All scale lines 1 mm. Scale a: Figs. 35, 39, 40, scale b: Figs. 33, 34, 36-38.

short (Fig. 38). Very short microscopic hairs in short, distinctly separated rows on dorsum and venter (Fig. 40), single on pleura. Microscopic hairs on dorsum longer around bases of macrosetae and on segment VIII; narrow areas without microscopic hairs ("setal imprints") originating from bases of D1-D3 and extending medioposteriorly for at least length of setae (Fig. 39). *Spiracular Disc:* Dorsal and lateral lobes subconical and subequal, lateral lobes dorsolateral (Fig. 33). Ventral lobes small, short, narrow basally, each with truncate apex and as wide as long (Fig. 34). Posterior surface of each dorsal lobe with extensive dark sclerite, extending from between spiracles to apex of lobe, distal one-third of lobe sclerotized anteriorly and posteriorly, apex of lobe an acute, anteriorly directed point (Fig. 34). Posterior surface of each lateral lobe with lateral sclerite, apex of lobe unsclerotized. Distal half of each ventral lobe with dark sclerite extending medially; at apex, a large seta arising from a pale spot; remainder of inner surface light brown (Fig. 35). Spiracles large, circular, outer circle

brown, inner circle black. Remainder of spiracular disc pale. Marginal band brown. *Anal Segment:* Four anal papillae, lateral papillae scarcely indicated, length ½ width or less, ventral papillae broadly rounded. Anal opening horizontal.

Specimens Examined: Eight larvae from 17.7 km E of Waterford, campground at Turlock Lake State Recreation Area, Stanislaus Co., California, J. K. Gelhaus, coll. (JKG).

Subgeneric Discussion: The heavily sclerotized dorsal lobes of *Hesperotipula,* with pointed, recurved apices, are similar to those found in the *T. (Lunatipula) fuliginosa* and *lunata* groups, *Triplicitipula* and *Vestiplex.* These groups also share other similarities, including a large amount of sclerotization on each lateral lobe (but with unsclerotized apex), reduced anal papillae and generally short, dark macrosetae in a similar arrangement. One exception to the overall similarity of macrosetae is found in seta D4, which is pale-tipped and appressed in *Hesperotipula* but is approximately the same size and in the same position as the completely dark D4 found in the other three groups. Additional relationships are seen between *Hesperotipula* and *Triplicitipula,* for both subgenera possess ventral lobes with truncated apices and similar patterns of sclerotization, and with "setal imprint" patterns in the arrangement of the microscopic hairs.

The distinctions between *Vestiplex* and *Hesperotipula* are straightforward and easily observed. *Vestiplex* possesses an added band between the anus and the anal papillae in addition to the marginal band around the anal segment and has, at most, only small sclerotized apical points on the dorsal lobes. *Hesperotipula* possesses only the marginal band and has well-developed curved points on the dorsal lobes. The separation of *Hesperotipula* from most species of *Lunatipula* is more difficult. The *T. (Lunatipula) fuliginosa* group differs from *Hesperotipula* primarily in the shape and sclerotization of the ventral lobes. In *Lunatipula,* these lobes are rounded at the apices, with some basal sclerotization, and lack the long seta at the apex of each.

Hesperotipula and *Triplicitipula* are not clearly distinguishable, and with only one species of *Hesperotipula* reared it is difficult to determine those characters most useful in the future for separating these groups. *Hesperotipula* does not have a dark spot at the base of the ventral lobe as do known species of *Triplicitipula.* The short microscopic hairs are arranged in short, distinctly separated rows, so that the overall effect in *Hesperotipula* is of sparser microscopic hairs than those found in *Triplicitipula.* This is reflected in the vague "setal imprints" of *Hesperotipula,* as the visibility of this feature is directly dependent on the density of the microscopic hairs. Seta D4 may also prove useful in separation of the two groups. This seta is pale-tipped and appressed in *Hesperotipula;* in *Triplicitipula,* it may be long or short but is completely dark.

Habitats of *Hesperotipula:* Twenty-one nearctic species are included in *Hesperotipula;* all are endemic to western North America, and most are found only in California. Habitat information is available for only two species.

The larvae of *T. aitkeniana* were collected at the upper end of a small ravine, on a slight slope under a few large trees, in the top 2 cm of damp, sandy soil under a 2.5 to 4.0 cm layer of fig, oak and horsechestnut leaves. I collected pupae of *T. linsdalei* in California from rocky soil under a deep layer of leaves, on a small hillside with alder and oak trees.

Subgenus *Lunatipula* Edwards

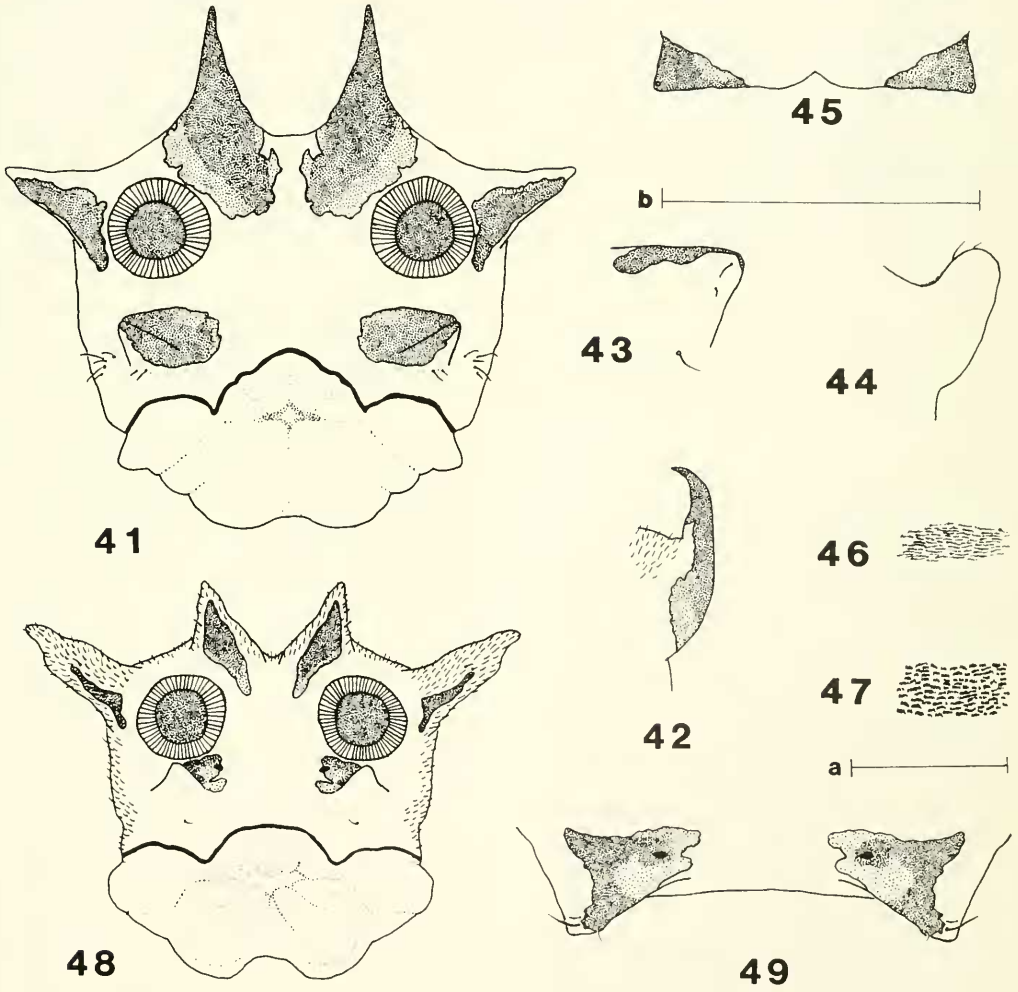
I have examined larvae reared and associated with adults for eight species of nearctic *Lunatipula.* Three of these species, *Tipula fuliginosa, T. morrisoni* and *T. disjuncta,* are described below to illustrate some of the variety of form found within the subgenus.

Tipula (Lunatipula) fuliginosa (Say)

Description: Length 27.2-29.0 mm, width 4.6-4.7 mm, body brownish white. *Abdomen:* All macrosetae blackish brown, setae D1-D3 and D6 long, D4 and D5 very short (Fig. 50). Setae L1 and L4 long, L2 and L3 very short and appressed (Fig. 52). Setae V2-V5 long, V1 very short (Fig. 51). Short microscopic hairs in short to long rows on dorsum and venter (Fig. 46),

single on pleura. *Spiracular Disc:* Dorsal and lateral spiracular lobes subconical, lateral lobes dorsolateral, length of lateral lobes ⅔ length of dorsal lobes (Fig. 41). Ventral lobes small, triangular in posterior aspect, each apex with curved margin, basal width of each twice its length (Fig. 43). Posterior surface of each dorsal lobe with complete dark sclerite extending from between spiracles to apex of lobe; distal half of lobe sclerotized anteriorly and posteriorly, apex of lobe an acute, anteriorly directed point (Fig. 42). Posterior surface of each lateral lobe with triangular dark sclerite, from near spiracles to near unsclerotized apex, lobe apex unsclerotized. Inner surface of each ventral lobe with complete dark sclerite, extending to outer surface (Fig. 45). Spiracles large, circular and black. Remainder of spiracular disc pale. Marginal band brown. *Anal Segment:* Four anal papillae, lateral papillae small, basal width twice length, ventral papillae broadly rounded.

SPECIMENS EXAMINED: Five larvae from Baldwin Woods, Breidenthal Reserve, 17.7 km SE of Lawrence, Douglas Co., Kansas, J. K. Gelhaus, coll. (JKG).



Figs. 41-43, 45, 46. *Tipula (Lunatipula) fuliginosa.* 41, spiracular area. 42, dorsal spiracular lobe, lateral aspect. 43, ventral spiracular lobe, lateral aspect. 45, ventral lobes, dorsal aspect. 46, example of microscopic hairs on dorsum of abdomen. Figs. 44, 47-49. *T. (L.) morrisoni.* 44, ventral spiracular lobe, lateral aspect. 47, same area as Fig. 46. 48, spiracular area. 49, ventral lobes, dorsal aspect. All scale lines 1 mm. Scale a: Figs. 41, 42, 45, 48, scale b: Figs. 43, 44, 46, 47, 49.

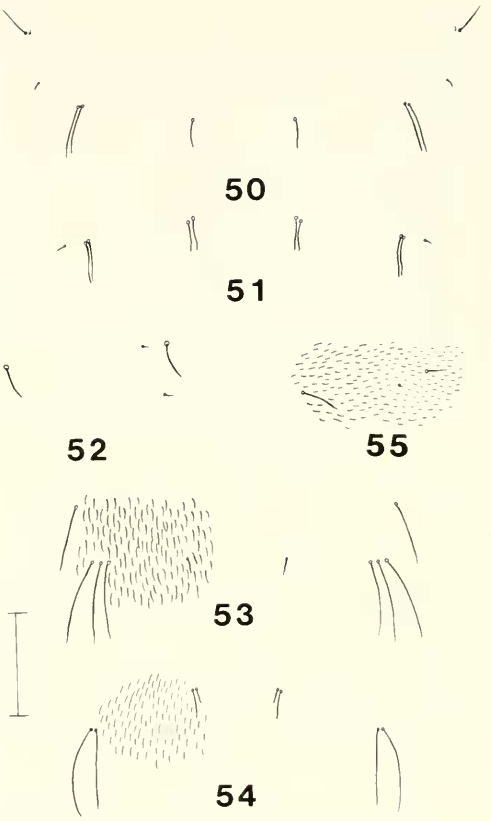
Tipula (Lunatipula) morrisoni Alexander

Description: Length 24.6-28.6 mm, width 3.4-4.3 mm, body gray brown. *Abdomen:* Macrosetae as in *T. fuliginosa* (Figs. 50-52). Short microscopic hairs in subequal short rows on dorsum and venter (Fig. 47), single or in small groups on pleura. *Spiracular Disc:* Dorsal and lateral spiracular lobes subconical, lateral lobes dorsolateral, length of lateral lobes twice length of dorsal lobes (Fig. 48). Ventral lobes small, triangular in posterior aspect, each with rounded apex, basal width twice length (Fig. 44). Posterior surface of each dorsal and lateral lobe with dark sclerite, on dorsal lobes extending from below base to near apex, apex of lobe unsclerotized; sclerite on lateral lobe extending from near base to midlength of lobe. Remainder of dorsal and lateral lobes with single, long microscopic hairs. Inner surface of each ventral lobe extensively sclerotized, darkest area "L"-shaped (Fig. 49). Spiracles large, circular, inner circle black, outer ring brown. Remainder of spiracular disc pale. Marginal band brown. *Anal Segment:* Four anal papillae, all broadly rounded and scarcely evident.

Specimens Examined: Seven larvae from the following localities in KANSAS: Douglas Co., Hole-in-the-Rock, 8.0 km W of Baldwin City, J. K. Gelhaus, coll. (JKG); Miami Co., at Miami Co. State Lake, 4.0 km E of Fontana, J. K. Gelhaus, coll. (JKG).

Tipula (Lunatipula) disjuncta Walker

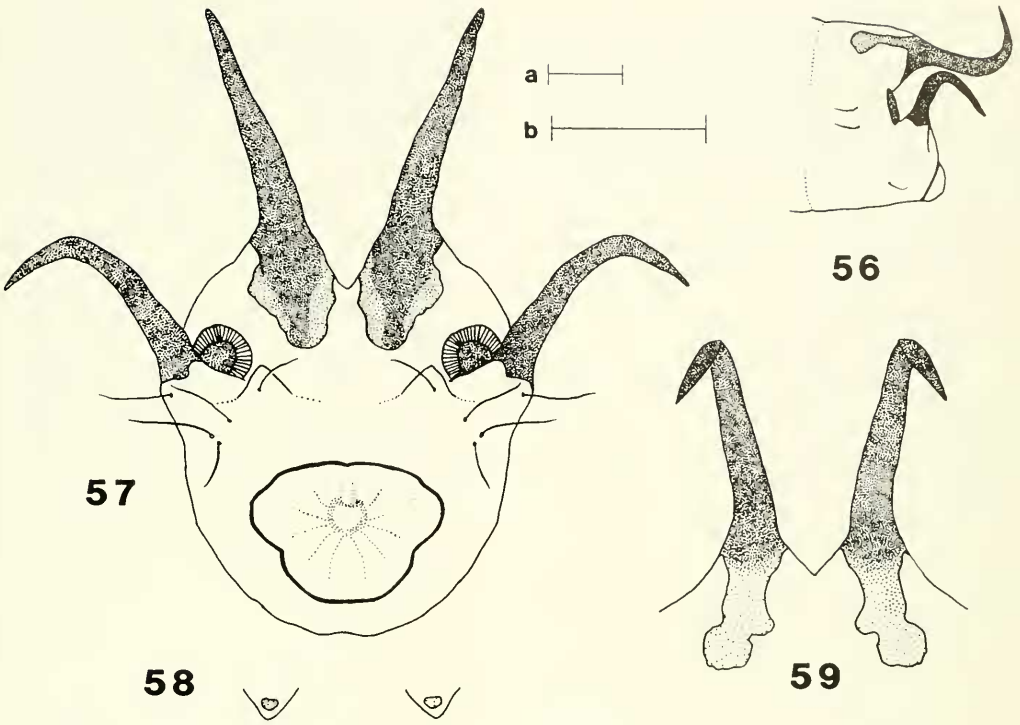
Description: Length 22.9 mm, width 4.3 mm, body yellowish white. *Abdomen:* All macrosetae golden-yellow setae D2-D4 and D6 very long, D1 short and inconspicuous, D5 absent (Fig. 53). Setae L4 very long, L1 short, L2 vestigial, L3 absent (Fig. 55). Setae V2 and V3 very long, V4 and V5 shorter, V1 absent (Fig. 54). Dorsum with golden-yellow macroscopic hairs, single and appressed (Fig. 53), slightly shorter on pleuron and venter (Figs. 54, 55). *Spiracular Disc:* Dorsal and lateral spiracular lobes completely sclerotized, forming smooth, curved hooks (Fig. 57), dorsal hooks longer, each dorsal lobe curved cephalad, each lateral lobe curved ventrad (Fig. 56). Sclerotization of lobes mostly reddish-brown, blackish distally. Sclerite of dorsal lobes extending basally between spiracles, anteriorly onto eighth abdominal tergite (Fig. 59). Ventral lobes small, triangular in posterior aspect, basal width of each 1.5× its length. Inner surface of each ventral lobe with pale tan, circular sclerite (Fig. 58). Spiracles small, circular, black and widely separated. Remainder of spiracular disc pale. Marginal band thin, pale brown. *Anal Segment:* Anal segment small, lobes of anal papillae indistinct.



Figs. 50-52. *Tipula (Lunatipula) fuliginosa,* abdominal macrosetae. 50, dorsal setae. 51, ventral setae. 52, pleural setae. Figs. 53-55. *T. (L.) disjuncta,* abdominal macrosetae. 53, dorsal setae and example of hairs. 54, ventral setae and example of hairs. 55, pleural setae and hairs. Scale line 1 mm.

Specimens Examined: One larva from University of Kansas Natural History Reservation, 8.0 km NE of Lawrence, Douglas Co. Kansas, C. W. Young, coll. (KU).

Subgeneric Discussion: *Lunatipula* is the largest subgenus of *Tipula,* containing approximately 130 species in North America. The larvae of only ten of these species are known: three from the larval descriptions presented here, reared material for five additional species, and two from the literature *(T. usitata,* Alexander, 1920; *T. bicornis,* Forbes, 1890). The larvae of eleven palearctic species of *Lunatipula* have been described. At least three groups appear



Figs. 56-59. *Tipula (Lunatipula) disjuncta.* 56, terminal abdominal segments, lateral aspect. 57, spiracular area. 58, ventral spiracular lobes, dorsal view. 59, dorsal lobes and dorsum of abdominal segment VIII. All scale lines 1 mm. Scale a: Fig. 56, scale b: Figs. 57-59.

easily separable based on 21 species: (1) *T. bicornis, morrisoni* and the palearctic *T. vernalis,* (2) *T. disjuncta,* the palearctic *T. livida* and *lesnei,* (3) and the remainder of the reared species of *Lunatipula (T. australis, dietziana, duplex, fuliginosa, oxytona, translucida, usitata)* and the palearctic *T. lunata* group.

The most distinctive feature of all *Lunatipula* is the sclerotization of the dorsal lobes, varying from a moderate amount but with unsclerotized apices in the *T. bicornis* group, a considerable sclerotization forming short, curved apical points in *T. fuliginosa* and others, to a complete sclerotization forming long, curved hooks in the *T. disjuncta* group. The lateral lobes show a similar progression of sclerotization, from small sclerites in the *T. bicornis* group to completely sclerotized curved hooks in the *T. disjuncta* group. The ventral lobes are short, broad and triangular, with various patterns of sclerotization; pale in the *T. disjuncta* group but darker and more distinct in the remaining species of *Lunatipula.* The lateral and ventral anal papillae are distinct lobes in the palearctic *T. peliostigma* and *T. soosi,* weakly developed in *T. morrisoni* and *T. fuliginosa* and absent entirely in *T. disjuncta.*

The length and arrangement of the macrosetae are similar in the *T. bicornis* and *T. fuliginosa* groups, both groups possessing very short V1, D4 and D5 setae, and all the setae dark brown. In contrast, in the *T. disjuncta* group, the macrosetae are yellowish, noticeably elongate, and D5 and V1 are absent. Additionally, this latter group has only long, single, yellow macroscopic hairs. Both the *T. bicornis* and *T. fuliginosa* groups have a predominance of short microscopic hairs arranged in short rows.

Sclerotized, acutely pointed dorsal lobes are found to a similar degree in the *T. fuliginosa* group, *Triplicitipula, Hesperotipula* and some species of *Vestiplex.* By com-

parison, the smaller sclerites of the dorsal and lateral lobes found in the *T. bicornis* group resemble those of *Serratipula, Pterelachisus* and certain other species of *Vestiplex.* The small, triangular ventral lobes as seen in all *Lunatipula* are similar to those in *Vestiplex, Serratipula* and *Pterelachisus.* A predominance of short microscopic hairs, small but still distinct anal papillae and dark, short macrosetae are found in *Lunatipula* (excluding the *T. disjuncta* group), *Vestiplex, Serratipula,* and *Pterelachisus.*

The *T. disjuncta* group is distinct from other species groups of *Lunatipula* in many characters and shows close similarities only to the subgenus *Odonatisca;* in fact, the two groups are nearly indistinguishable. Both groups possess completely sclerotized, hook-like dorsal and lateral lobes, small ventral lobes, no distinct anal papillae, a predominance of macroscopic hairs and elongate, yellowish macrosetae. *Tipula disjuncta* and *T. livida* do have sclerotization on the eighth abdominal tergum, but at least one species in this group, *T. lesnei,* and the subgenus *Odonatisca,* lack this. It may be possible to separate these two groups using the distinctions listed in the discussion of *Odonatisca.*

Serratipula is generally similar to the *T. bicornis* group but differs in a number of features. In *Serratipula,* D4 is long, the lateral papillae are pronounced, the inner surface of each ventral lobe is almost completely sclerotized, and the spiracles are brown; moreover, most of the species occur only in California. In contrast, in the *T. bicornis* group, D4 is short, the papillae are reduced, the inner surface of each ventral lobe has a C-shaped sclerotized pattern, and the inner circle of each spiracle is black; also, none of the species in this group occur in California so far as known.

The *T. fuliginosa* group, *Triplicitipula* and *Hesperotipula* are similar in overall morphology, but the latter two subgenera possess truncated, heavily sclerotized ventral lobes and dense microscopic hairs. The *Tipula fuliginosa* group has ventral lobes with more rounded apices, and the microscopic hairs are never dense.

HABITATS OF *LUNATIPULA:* All the larvae known for this subgenus have been found in terrestrial habitats. I collected larvae of *T. fuliginosa* in Kansas from under a thick layer of leaf litter on a hilltop in an oak-hickory woods. Rogers (1942) also reared this species in Michigan from an oak-hickory woods. Alexander (1920) cited larvae of *T. fuliginosa* as "living in debris under the nest of a turkey vulture" in Maryland.

Larvae of *T. disjuncta* were collected in Kansas by C. W. Young from rich woodland soil with many pieces of rotting wood. Rogers (1942) found larvae of this species in oak-hickory woods in Michigan from "damp but friable sandy loam, just beneath the coarser leaf mold." A larva similar to *T. disjuncta,* described by Alexander (1920), as Tipulinae no. 2, was found under a rock in a field. The larvae of the palearctic species *T. livida* and *lesnei* are similar in morphology to *T. disjuncta.* Chiswell (1955) found the larvae of *T. livida* "under loose, damp moss on the floor of a beechwood" and also under moist leaf mold. Theowald (1967) additionally records *T. livida* from rotting wood. Hemmingsen (1958) collected *T. lesnei* in moist canyons, from soil 5-15 cm deep and rich in roots.

I have made two separate collections of the larvae of *T. morrisoni,* both in the upper 40 cm of soil under leaf litter in mixed deciduous woodlands. The larvae of the nearctic *T. bicornis* and the palearctic *T. vernalis,* although similar to that of *T. morrisoni* (in fact, all three are included in the same species group on the basis of adult characters), have not been found in wooded areas. Rogers (1942) wrote that the larvae of *T. bicornis* "are frequently abundant or even pests in meadows and fertile grasslands." Young (1978) collected pupae in Kansas from "grassland, about 6 mm beneath the ground surface, which was covered by a thin mat of mosses." The larva of *T. vernalis* has also been collected from grassland, occasionally as a pest in cultivated grasses, but also from borders of woodlands, the litter layer of shrubs, and once in water (Theowald, 1967; Chiswell, 1956).

Most of the other species of *Lunatipula* were reared from woodland habitats, specifically from the top layer of soil under leaf litter. Alexander (1920), however, recorded the larva of *T. usitata* from beneath the bark of a fallen tree, but it also has been reared from a "pile of dead cypress needles on roof" and from "moss found on county road" (Alexander, 1967). *Tipula oxytona*, in Florida, was found in "friable, sandy soil, usually within 50 mm of surface but as deep as 200 mm in dry seasons; larvae feed on rootlets of wire grass" (Rogers, 1933). The palearctic *T. alpina* and *T. selene* have both been reared from rotting wood and debris (Chiswell, 1956). *Tipula cava* and *T. fasciapennis* were each collected once from old cow dung (Theowald, 1967).

Subgenus *Nippotipula* Matsumura

Tipula abdominalis is the only species of this subgenus for which I have examined reared larvae associated with adults.

Tipula (Nippotipula) abdominalis (Say)

Malloch 1917:200, figures (as *Tipula* sp. 2).
Alexander 1920:1011-1013, Figs. 536-537.

Description: Length 50.1-60.1 mm, width 7.0-9.0 mm, body light brown to brownish gray. *Abdomen:* Posterior annulus of each segment I-VII with conspicuous dorsal and ventral transverse swellings (Fig. 62), dorsal swellings twice as wide as high, ventral swellings slightly higher. Segment VIII with one or two pairs of pleural tubercles (Fig. 62), each posterior tubercle slightly longer than width at base, a dark macroseta at apex; anterior tubercles shorter. Most macrosetae black. Setae D2-D4 long, D1, D5 and D6 shorter, D6 pale and branched (Fig. 63). Setae L2 and L4 long, L1 short, L3 of medium length, pale and branched, L1-L3 often on a slight swelling (Fig. 62). Setae V3 and V4 long, V5 and V1 slightly shorter, V1 pale brown, V2 absent (Fig. 64). Body with short microscopic hairs in groups of two or three (Fig. 61). *Spiracular Disc:* All spiracular lobes generally elongate and subconical, lateral lobes equidistant from dorsal and ventral lobes; dorsal lobes short, length twice width at base; lateral lobes longer, about 1.25× length of dorsal lobe; ventral lobe slightly more than 1.5× as long as of dorsal lobes (Fig. 60). Posterior surface of each dorsal lobe with a thin, vertical sclerite, darkest laterally, with border of small groups of black setae. Basal half of posterior surface of each lateral lobe with border of black setae, increasing in length distally; a thin, medial sclerite on lobe. Apex of lateral lobe bifurcated; outermost tip with dark macroseta, both tips with clusters of macroscopic hairs. Basal 0.8 of posterior surface of each ventral lobe with border of small groups of black setae, increasing in length distally; a long black seta at distal end of border. Apex of ventral lobe often bifurcated, one macroseta and macroscopic hair cluster at each apex. Remainder of spiracular disc, including all lobes, with short microscopic hairs. Two pairs of accessory lobes: one lobe anterior to area between dorsal and lateral lobes on each side, with two or three distinct tips; one lobe anterior to area between lateral and ventral lobes on each side, with three tips. Spiracles small, thick, circular and brown, widely separated by 3× or more diameter of a spiracle. Marginal band black. *Anal Segment:* Six, elongate anal papillae (Fig. 62), lateral papillae single, median papillae paired, length/basal width 3-4.

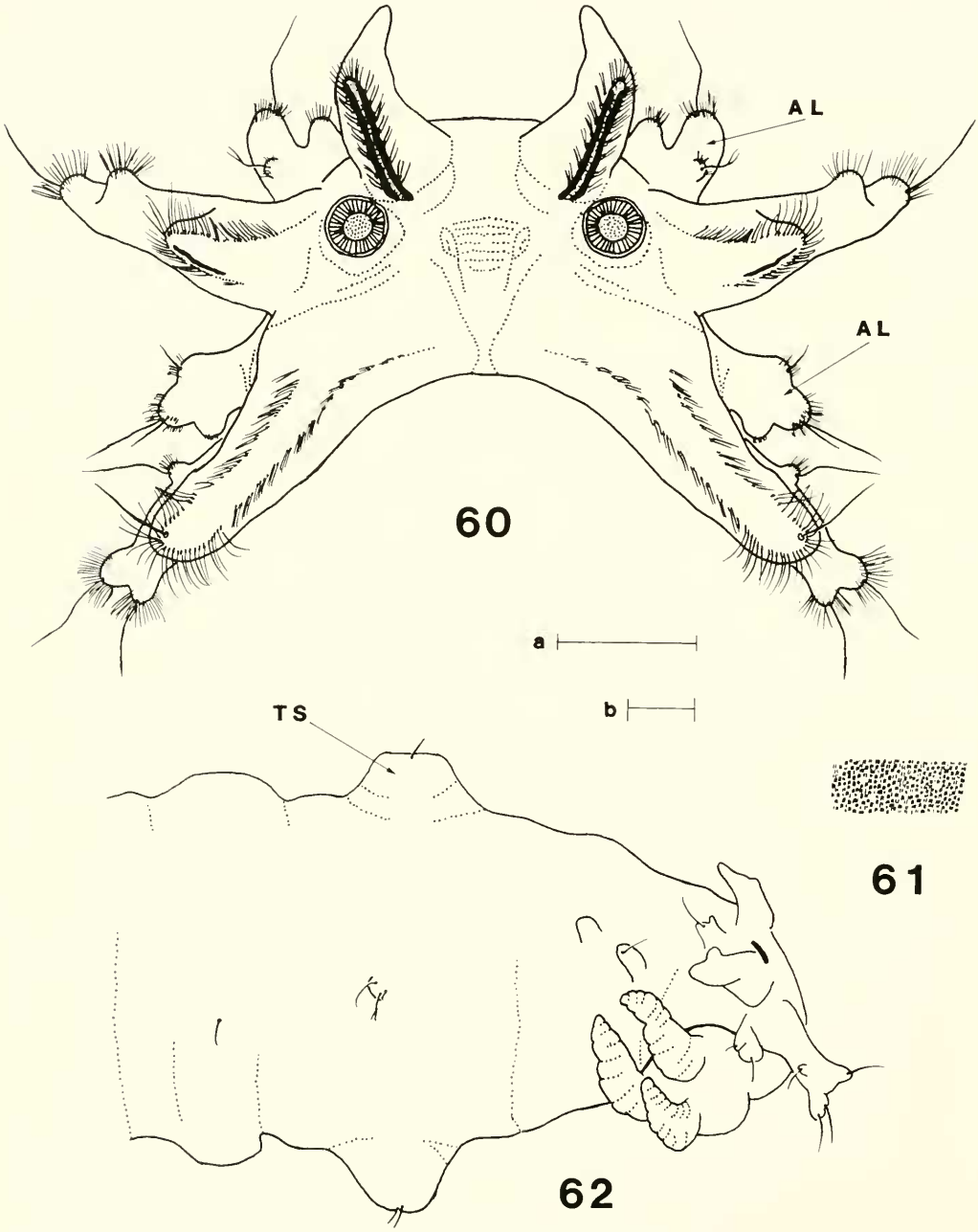
Specimens Examined: Ten larvae associated with adults from the following localities: KANSAS: Chautauqua Co., branch of Turkey Creek, 1.6 km SE of Chautauqua, J.K. Gelhaus, coll. (SBSK); Cherokee Co., unnamed spring, 4.0 km S of Galena, J.K. Gelhaus, coll. (SBSK); NEW YORK: Tompkins Co., Locke Creek, Ludlowville, H. Teskey, coll. (CNC); Tompkins Co., Cascadilla Creek, Ithaca, C.P. Alexander, coll. (UM).

Subgeneric Discussion: *Tipula abdominalis* has a distinctive spiracular disc. The spiracular lobes are subconical and almost totally unsclerotized, with the disc completely covered with short microscopic hairs. The dorsal lobes are shorter than either the lateral or ventral lobes, and none of the lobes has the ability to close over the spiracles. The accessory lobes between and anterior to the dorsal and lateral lobes and between and anterior to the lateral and ventral lobes are unique. Each of these accessory lobes has apical clusters of macroscopic hairs and one or a few macrosetae. Small, dark, narrow sclerites are found on the dorsal and lateral lobes and the setal border of the spiracular lobes is vestigial. The spiracles are small, circular, widely separated, and appear thick and slightly raised above the cuticular surface.

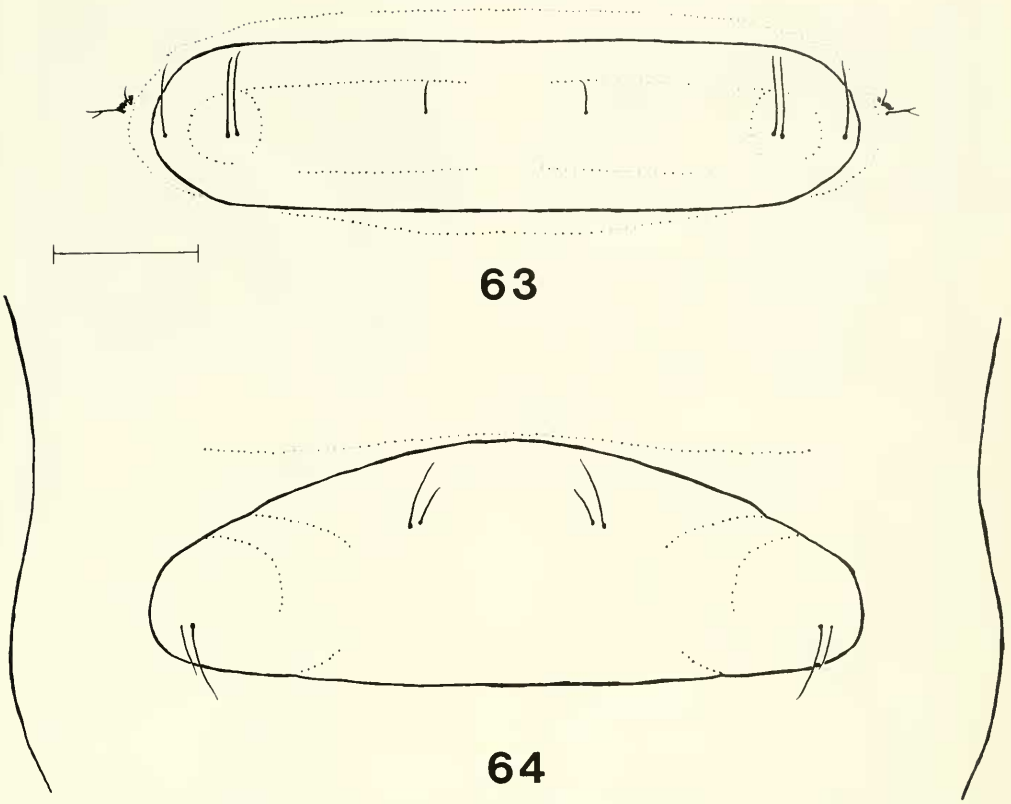
Each of the first seven abdominal segments possesses dorsal and ventral transverse swellings, and the eighth segment has

one or two pleural tubercles. Like the spiracular disc, the rest of the abdomen is covered with short microscopic hairs, but also noticeable here is the complete lack of any macroscopic hair. Seta V2 is absent and there are six, long anal papillae.

The general shape of the spiracular lobes, the overall lack of sclerotization of the spi-



Figs. 60-62. *Tipula (Nippotipula) abdominalis.* 60, spiracular area; AL-accessory lobe. 61, example of abdominal microscopic hairs. 62, terminal abdominal segments, lateral aspect; TS-transverse swelling. All scale lines 1 mm. Scale a: Figs. 60, 61, scale b: Fig. 62.



Figs. 63, 64. *Tipula (Nippotipula) abdominalis,* abdominal macrosetae. 63, dorsal setae on transverse swelling. 64, ventral setae on transverse swelling. Scale line 1 mm.

racular disc and the predominance of short microscopic hairs on it, and the inability to close the lobes over the spiracles all show similarities to the corresponding structures of *Arctotipula.* Additionally, the presence of cuticular swellings on abdominal segments I-VII, the small, widely separated spiracles and the absence of appreciable macroscopic hairs are characteristics shared by *Arctotipula, Sinotipula* and *Nippotipula.* The abdominal swellings are transverse ventrally in both *Nippotipula* and *Sinotipula* but are also found dorsally in *Nippotipula. Arctotipula* has lateral and ventral conical swellings. *Nippotipula* has only a vestigial setal border around the spiracular lobes, although a well-developed setal border is found in most other aquatic *Tipula* except for *Arctotipula.* Branching of the lateral and ventral spiracular lobes into outgrowths with apical setae and hair clusters, and the presence of accessory lobes are distinctive for *Nippotipula.* Some *Arctotipula* have apical clumps of macroscopic hair and setae on the lateral and ventral lobes, but lack the additional swellings on the spiracular lobes as well as the accessory lobes.

HABITATS OF *NIPPOTIPULA:* Only two nearctic species are included in *Nippotipula,* the well known *T. abdominalis* and the relatively recently described *T. metacomet.* Only the larva of *T. abdominalis* has been reared and associated with the adult, and the possibility exists that the larva of the sympatric *T. metacomet* has been confused with that of *T. abdominalis.*

The larvae of *T. abdominalis* are stream dwellers. Rogers (1942) collected the species in Michigan from the "leaf drift of two small sandy brooks" and in Florida (Rogers, 1933), from "among leaf drift and matted rootlets of sand bottom streams or in sand of stream bottom." Alexander (1920) found larvae "abundant under satu-

rated decaying leaves or under tussocks of grass at the edge of the water." In Kansas, I have found the larvae most abundant in rocky or gravel-bottomed streams in heavily wooded areas; they are usually in leaf packs, under rocks, or even among mats of watercress. These streams may be permanent or intermittent.

Subgenus *Nobilotipula* Alexander

Larvae of both nearctic species in this subgenus, *Tipula nobilis* and *T. collaris,* have been described. Since *T. collaris* has been previously illustrated, I will redescribe and illustrate *T. nobilis* here.

Tipula (Nobilotipula) nobilis (Loew)

Alexander 1920:1004, Fig. 507.

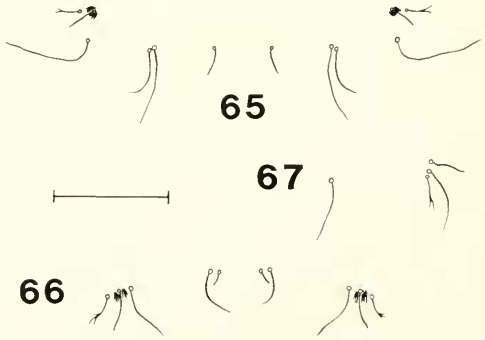
Description: Length 19.7-20.6 mm, width 2.7-3.3 mm, body yellowish brown. *Abdomen:* Most macrosetae brown, setae D2 and D4 long, D3 of medium length, D1, D5 and D6 short, D6 pale and branched (Fig. 65). Setae L2 and L4 long, L1 and L3 shorter and pale, L3 branched; L1-L3 in approximately vertical alignment (Fig. 67). Setae V3 and V4 long, V1, V2 and V5 shorter, V1 branched (Fig. 66). Microscopic hairs single, flattened, broad, scale-like and reflective (Fig. 70,71), shortest hairs appressed to body, longer hairs often perpendicular to body, hair clusters around setae D5 and V2. *Spiracular Disc:* All spiracular lobes subequal, slightly longer than width at base, lateral lobes equidistant from dorsal and ventral lobes (Fig. 68). Lobes with well-developed border of setae, longest setae approximately equal to basal width of lobe. Posterior surface of each lobe with extensive light brown sclerite. Each ventral lobe with narrowly triangular, dark, median line; two dark spots near base. Spiracles brown, inner circle with dark irregular transverse pattern. Remainder of spiracular disc pale. Marginal band light brown. *Anal Segment:* Segment large, anal opening transverse; six elongate anal papillae, anterior papillae paired, posterior papillae single (Fig. 69); lateral papillae length/basal width 5.0-5.5.

Specimens Examined: Five larvae from the following two localities: MAINE: Penobscot Co., Orono, C. P. Alexander, coll. (UM); QUEBEC: Gatineau Park, 16.1 km NW of Ottawa (Ontario), H. Teskey, coll. (CNC).

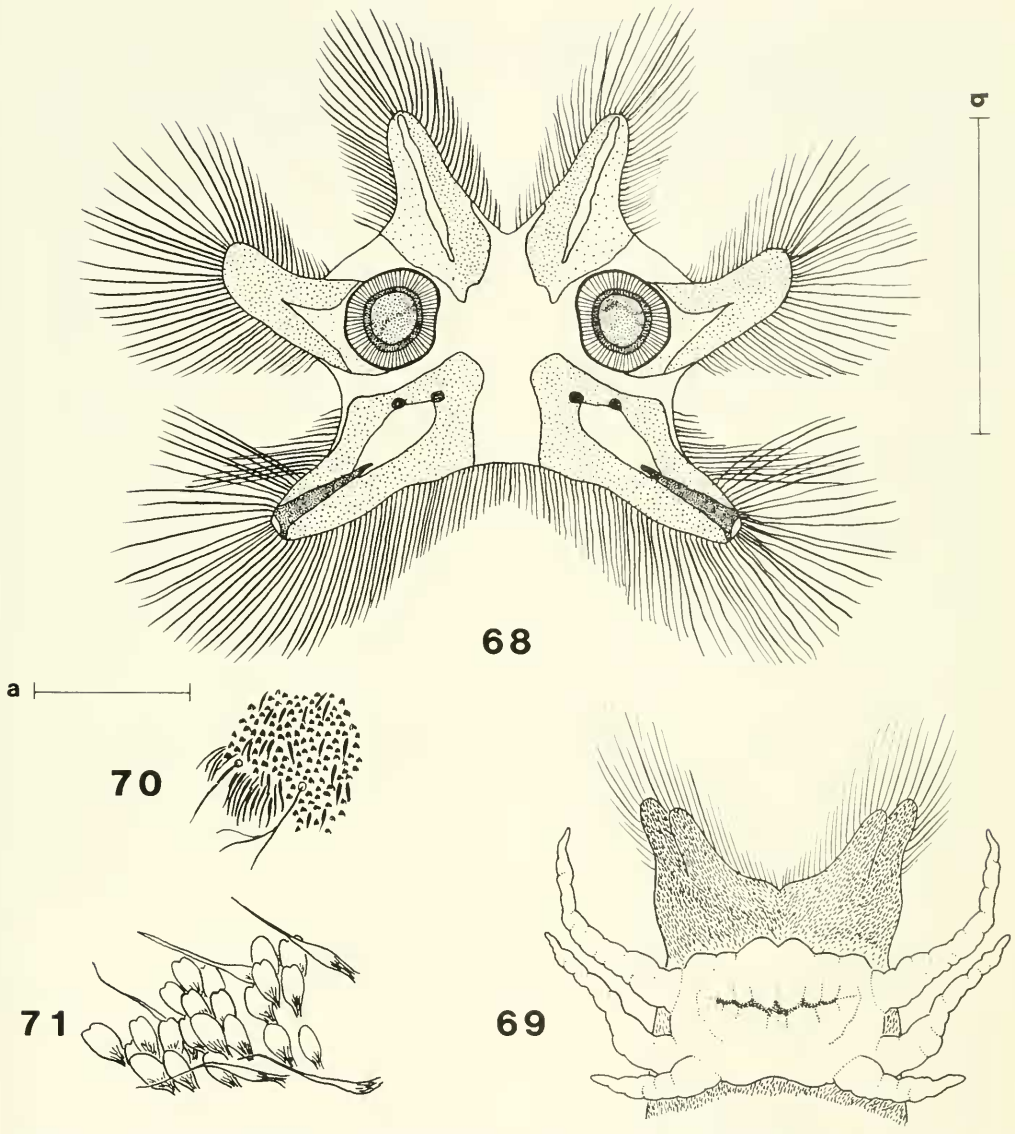
Subgeneric Discussion: The larvae of *Nobilotipula* possess two distinctive characters: the arrangement of the pleural abdominal macrosetae and the modified, lamelliform microscopic hairs. Most easily observable is the arrangement of setae L1-L3 in an approximately vertical alignment. This arrangement is also found in the palearctic *T. (Platytipula) melanoceros.* In all other known groups, and even in other species of *Platytipula* (e.g., *T. spenceriana*), seta L1 is caudad to seta L2, not above it. Although setae L1-L3 in *Angarotipula* are very close together, seta L1 is not directly dorsal to L2, but is slightly caudad to it.

The microscopic hairs in *Nobilotipula* are unique, being flattened and broad, with longitudinal ridges, and distinctly reflecting light (Fig. 71); those in other subgenera are cylindrical and narrow, without ridges, and not reflective. Two distinct lengths of microscopic hairs are seen in *Nobilotipula:* short microscopic hairs, which possess blunt, indented apices and are closely appressed to the body; and long microscopic hairs, with pointed apices that are often nearly perpendicular to the body. The hairs are usually singly placed, although in *T. collaris* the abdominal dorsum displays short rows of short microscopic hairs. These rows combine to form an overall arrangement of three pairs of circular areas anteriorly on each segment, followed by a pair of "comma"-shaped marks. In addition, the pleural microscopic hairs of this species are densely placed, giving the effect of a reddish-brown band on the abdominal pleuron.

Habitats of *Nobilotipula:* Alexander (1920) found larvae and pupae of *T. collaris*



Figs. 65-67. *Tipula (Nobilotipula) nobilis,* abdominal macrosetae. 65, dorsal setae. 66, ventral setae. 67, pleural setae. Scale line 1 mm.



Figs. 68-71. *Tipula (Nobilotipula) nobilis*. 68, spiracular area. 69, anal papillae, ventral aspect. 70, example of microscopic hairs and setae on abdomen. 71, microscopic hairs, 250×. Scale lines 1 mm. Scale a: Fig. 69, scale b: Figs. 68, 70.

beneath saturated moss (*Amblystegium irriguum* [Wils.] B. & S.) in New York. A larva and two pupae were collected by S. Hamilton and G. Schuster in North Carolina, from a small, fast-flowing, heavily shaded stream in a deciduous woodland.

Larvae of *T. nobilis* were collected by Alexander (1920) in Maine, from wet moss and also from decaying witch-hazel leaves. Additionally, H. Teskey collected larvae of *Tipula nobilis* from a woodland swamp in Quebec, and S. Teale found larvae in New York in shallow (2.5-5.0 cm deep), leaf-filled pools with a thick, organic silty bottom.

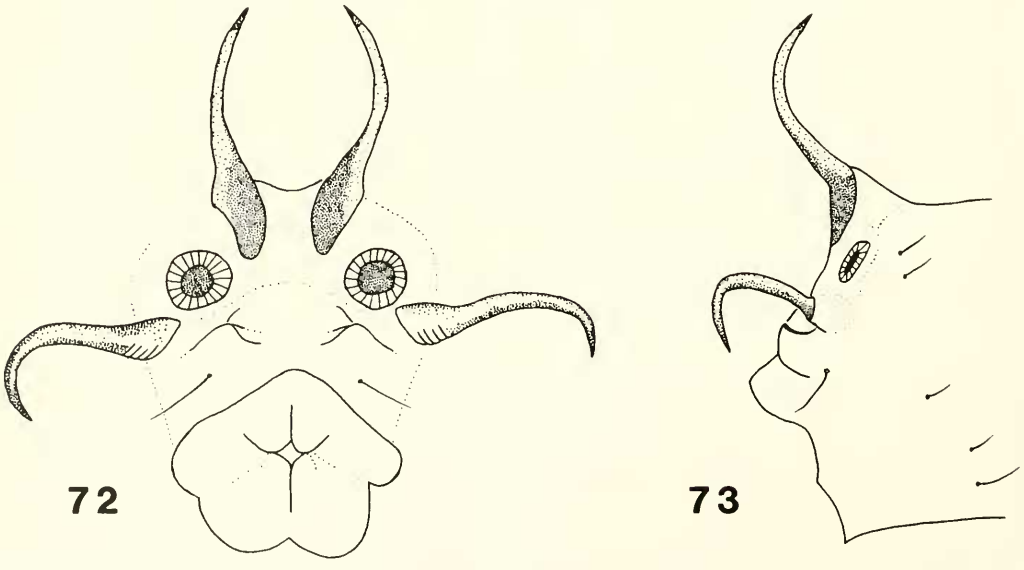
Subgenus *Odonatisca* Savchenko

Five nearctic species are included in this subgenus, three occurring in Alaska, one in the Pacific Northwest and one in southern Canada (Alexander, 1965). None of these species has been reared, but the larva of the palearctic *Tipula (Odonatisca) juncea* is known. I have not seen specimens of this species but know it from the brief descriptions of Hemmingsen (1959) and Theowald (1967).

The dorsal and lateral lobes of *T. juncea* are completely sclerotized, recurved hooks (Figs. 72, 73, redrawn from Theowald, 1967). The ventral lobes are small, triangular in posterior aspect, with the inner dorsal surface darkly sclerotized. The lateral and ventral anal papillae are greatly reduced and broadly rounded. The pattern of the abdominal macrosetae is apparently as in the *T. (Lunatipula) disjuncta* group (Figs. 53-55) except that possibly setae D1, V4 and V5 are long (Hemmingsen, 1959, Fig. 7c). The body is covered with yellowish, long microscopic hairs.

The larvae of *Odonatisca* are similar to those of certain *Lunatipula,* specifically *T. disjuncta* and the palearctic *T. livida* and *T. lesnei.* All of these possess hook-like dorsal and lateral lobes and reduced ventral lobes. The anal papillae are reduced and the macrosetal placement and length are generally alike in all these species. In fact, Theowald (1967) considers *T. juncea* and *T. lesnei* indistinguishable as larvae. Although *T. lesnei* is palearctic, it is similar to an unassociated larva from New York described by Alexander (1920, as Tipuline no. 2).

There are apparent differences between *Odonatisca* and the *T. (Lunatipula) disjuncta* group. *Tipula disjuncta* and *T. livida* have the sclerotization of the dorsal lobes extending onto the eighth abdominal tergum (Fig. 59) and a light sclerite on the inner surface of each ventral lobe (Fig. 58). There is no sclerotization on the eighth tergum in *T. lesnei* and *T. juncea* (Fig. 73), and the inner surfaces of the ventral lobes are entirely dark. Hemmingsen (1959:61) outlines a character to separate *T. lesnei* and *T. juncea.* He notes that the lateral lobes are curved downward in *T. lesnei* but the corresponding lobes of *T. juncea* are curved anteriorly (this distinction is not supported by the illustrations of Theowald, 1967, nor is it discussed in that work). Additionally, Hemmingsen shows second-instar larvae of *T. juncea* with macrosetae D1, V4 and V5 equal in length to the other setae. If this is



Figs. 72, 73. *Tipula (Odonatisca) juncea.* 72, spiracular area. 73, terminal abdominal segments, lateral aspect. Both redrawn from Theowald, 1967.

equally true for mature larvae, then this feature would also distinguish *T. juncea* from *T. lesnei*.

Added in proof: Theowald van Leeuwen, University of Amsterdam, sent two larvae of *Tipula juncea* to me for examination. The characters of these larvae agree with those stated above except for the following emendations: ventral spiracular lobes with the inner dorsal surface lightly sclerotized and two dark spots at base; macrosetae as in *Tipula disjuncta* except seta D1 is ⅔× length of setae D2-D4 and seta L3 is present and subequal in length to seta L4; lateral spiracular lobes curved somewhat anteriorly.

Habitats of *Odonatisca:* Hemmingsen (1959) discussed the biology of *T. juncea* and related species. He collected larvae from an area of shifting sand in a dune forest. Theowald (1967) additionally found the larvae in dry to moderately wet forest soil.

No notes on habitats are available for any of the nearctic species, although adults of *T. (O.) pribilofensis* were collected from sand dunes in Alaska (Alexander, 1923).

Subgenus *Platytipula* Matsumura

Four nearctic species of *Platytipula* have been reared and associated with adults.

Tipula (Platytipula) spenceriana Alexander

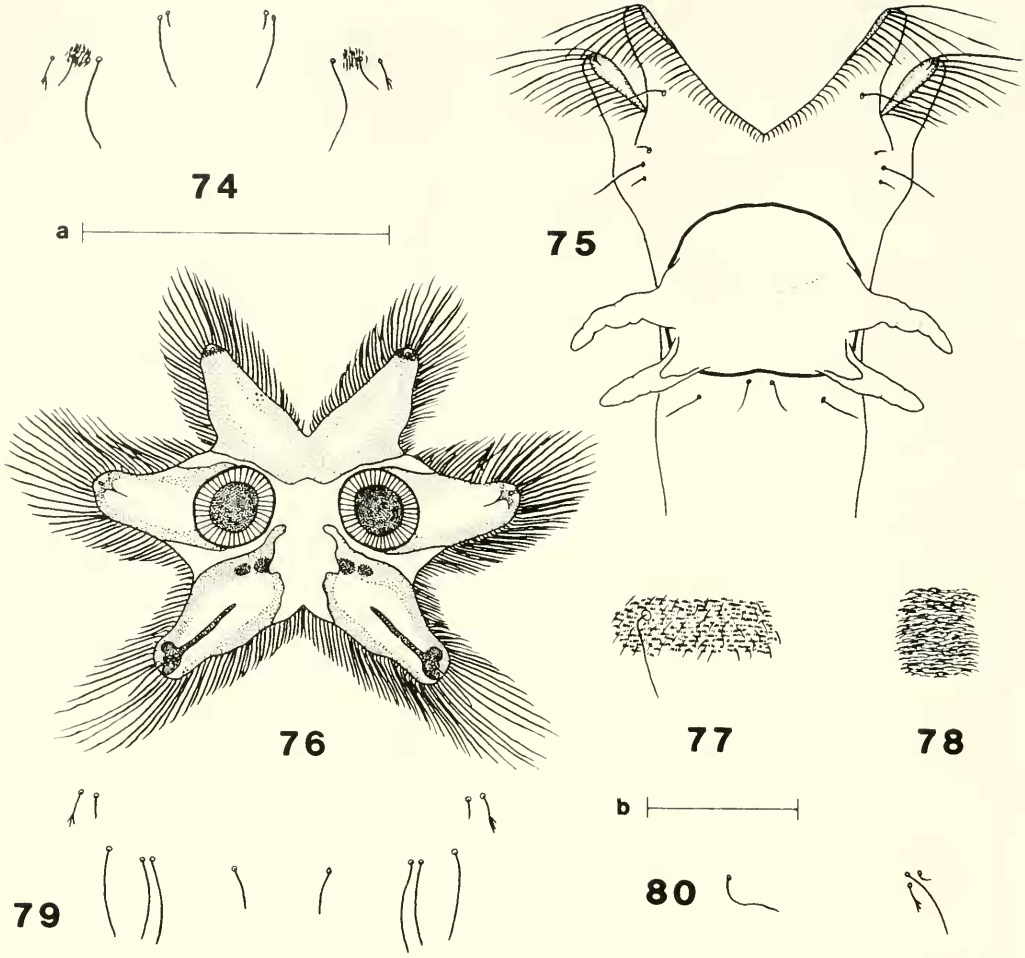
Description: Length 20.0-30.5 mm, width 2.3-2.6 mm, body yellow-brown. *Abdomen:* Most macrosetae dark brown, setae D2-D4 long, D1 and D6 shorter, D5 very short, D6 pale and branched (Fig. 79). Setae L2 and L4 long, L3 shorter, pale and branched, L1 very short (Fig. 80). Setae V3 and V4 long, V1 and V2 shorter, V5 very short, V1 pale and branched (Fig. 74). Very short microscopic hairs in long rows on dorsum and venter (Fig. 77), sometimes on pleura; single macroscopic hairs scattered between rows of microscopic hairs, long and most dense around bases of V2 and D2-D5. Pleura with dense, single macroscopic hairs (Fig. 78). *Spiracular Disc:* All lobes subequal, slightly longer than width at base, lateral lobes equidistant from dorsal and ventral lobes (Fig. 76). Lobes with well-developed border of setae, longest setae as long as basal width of lobes. Posterior surface of each lobe with brown sclerite, darkest at margins. Each ventral lobe with a dark, median line, approximately as long as lobe; two dark spots at base; a short, pale seta at apex. Each lateral lobe with a dark, median line, approximately ⅓ as long as lobe. Spiracles large, approximately circular, inner circle black, outer ring brown; distance between spiracles equal to diameter of a spiracle. Remainder of spiracular disc pale. Marginal band light brown. *Anal Segment:* Six anal papillae, four elongate, extending laterally or ventrally; two short; anteriormost papillae paired, posteriormost papillae single (Fig. 75); length/basal width of lateral papillae 2.5-3.5.

Specimens Examined: Ten larvae from Gravel Pit Lakes State Recreation Area, 24.1 km W of Cimarron, on U. S. Highway 64, Colfax Co., New Mexico, J. K. Gelhaus, coll. (JKG).

Subgeneric Discussion: I have examined larvae of three nearctic species of *Platytipula, T. paterifera, spenceriana* and *ultima,* as well as the descriptions of *T. ultima* (Young, 1981) and *cunctans* (Hyslop, 1910, as *infuscata*). The descriptions of three palearctic species of *Platytipula* are also available (for *T. autumnalis, luteipennis* and *melanoceros*).

Larvae of *Platytipula* are all similar in structure. The spiracular lobes are all subequal and of a medium length, with a well-developed border of long setae. All species possess a long, dark median line on each ventral lobe, and usually there is a short, median line on each lateral lobe. All six lobes usually have pale brown sclerites, darkest at margin. Also, there may be two dark spots at the base of each ventral lobe (these are fused into a dark line in the palearctic *T. luteipennis*). All the species have six anal papillae of which four are long and extended laterad or ventrad. The spiracles are large and often separated by less than the diameter of a spiracle.

The size and arrangement of the macrosetae varies among the species. Setae D2 and D3 may both be short (e.g., *T. melanoceros*) or long (e.g., *T. spenceriana*) or only D2 may be long (e.g., *T. luteipennis*). Setae D5 and D6 are short in *T. melanoceros* but are longer in all other species. Seta L1 is posterodorsal to L2 in most species, but is completely dorsal to L2 in *T. melanoceros*. Setae D6, V1 and L3 are branched in at least the nearctic species examined (not shown in Theowald, 1957, 1967, or Young, 1981). The body is covered with a combi-



Figs. 74-80. *Tipula (Platytipula) spenceriana.* 74, ventral abdominal macrosetae. 75, anal papillae, ventral aspect. 76, spiracular area. 77, example of microscopic hairs on dorsum of abdomen. 78, example of microscopic hairs on pleura of abdomen. 79, dorsal abdominal macrosetae. 80, pleural abdominal macrosetae. All scale lines 1 mm. Scale a: Figs. 77, 78, scale b: Figs. 74-76, 79, 80.

nation of both short microscopic hairs and macroscopic hairs; the microscopic hairs are in long rows with single macroscopic hairs scattered between the rows. The macroscopic hairs are most dense around the bases of the macrosetae and form a weakly developed cluster of hairs around setae V2; all the setae are clearly visible, though.

Larvae of *Platytipula* are similar morphologically to those of some aquatic subgenera, and present problems in separation from certain of these. The subequal, moderately long spiracular lobes with a well-developed border of long setae, the dark median line on each ventral lobe, elongate anal papillae, branched setae and the predominance of macroscopic hairs all can be found in other aquatic subgenera, including *Yamatotipula, Bellardina, Nobilotipula,* the palearctic *Acutipula* and *Emodotipula,* and the genus *Holorusia.* In particular, larvae of *Bellardina* and the genus *Holorusia* are most difficult to distinguish from those of *Platytipula.* The geographical range, specific habitat and overall body size may help in separating the three subgenera when used in conjunction with morphological characters found in the key.

Habitats of *Platytipula:* *Platytipula* contains 11 species in the Nearctic and many more species in the Palearctic. There is some life history information available for five nearctic species.

Larvae of *Tipula spenceriana* were found along a small, moderately flowing, seepage-stream, which ran for only 30 m before emptying into the Cimarron River, New Mexico. When first collected in mid-May, larvae in the second and third instars were found in wet mosses and algae in the stream. Less than one month later, the stream was greatly reduced in volume and rate of flow, and the larvae were mature.

Tipula ultima may also inhabit the margins of streams. I have made a number of collections of larvae in Kansas from dense leaf debris at the edges of small, slowly flowing streams, marshy areas and seepages. The species was collected from the mud of a well-shaded seep in Kansas (Young, 1981), and in the mud surrounding crayfish burrows of a glacial pothole in Illinois (Needham, 1903, as *T. flavicans*). Caudell (1913, as *T. flavicans*) collected pupae and adults in Virginia from a wet clayey area that had been previously inundated.

Larvae of *T. cunctans* have been reported twice from water-logged meadows (Hyslop, 1910; Rogers, 1933). At both times this species occurred in huge numbers, 200 larvae per square foot (2153 per square meter) as estimated by Hyslop, and caused damage by eating the roots and shoots of pasture grasses and clover. *Tipula maritima* also was collected from a similar meadow habitat in Indiana (J. S. Rogers, field notes). I have also found larvae of *T. cunctans* in Kansas from the clay margins of a shaded, small pond and marsh. Pupae of *T. pendulifera* were found in spongy, damp soil of an open slope surrounding a montane pond in Colorado. Pupae were usually found in burrows 51-63 mm deep, under mats of mosses (G. W. Byers, field notes).

The larvae of the palearctic species inhabit similar aquatic situations, most commonly in marshy soil or Sphagnum moss (Brindle, 1959; Theowald, 1967).

Certain generalizations can be made about life histories of known *Platytipula.* In the four species I have reared, larvae are often indicative of aquatic habitats that exist primarily in winter or early spring and dry considerably or entirely during the summer. As noted by Hyslop (1910), Young (1981) and myself, larvae develop rapidly during early spring and diapause throughout the summer in an inactive state out of water, pupating in the fall.

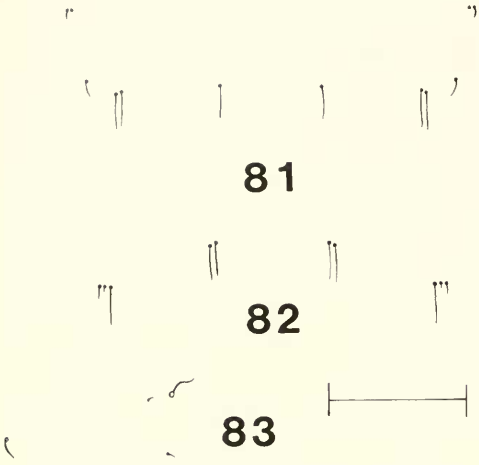
Subgenus *Pterelachisus* Rondani

Tipula (Pterelachisus) trivittata is the only nearctic species of this subgenus for which I have examined reared and associated larvae.

Tipula (Pterelachisus) trivittata Say

Greene 1909:289-290, Figs. 2-3. Alexander 1920: 1009-1010, Fig. 529. Alexander and Byers 1981: Fig. 71.

Description: Length 22.7-29.6 mm, width 2.7-3.6 mm, dorsum and venter light brown, pleura paler. *Abdomen:* Most macrosetae dark brown, setae D1-D3 long, D4 and D6 short, D5 pale and vestigial (Fig. 81). Setae L1 and L4 long, L2 and L3 very short, L1 dorsolateral to L2 (Fig. 83). Setae V3-V5 long, V1 and V2 short, close to V3 (Fig. 82). Short microscopic hair, in short, transverse rows of few to many hairs on dorsum and venter (Fig. 86), short microscopic hair in regularly spaced groups of one to few on pleura. *Spiracular Disc:* Dorsal and lateral lobes conical, dorsal lobes 3/4 length of lateral lobes, lateral lobes dorsolateral (Fig. 84). Dorsal and lateral lobes anteriorly with single spaced microscopic hairs, two dark macrosetae on posterior surface of each lateral lobe, 1/2 to 1/3 length from lobe tip. Dark brown, roughly triangular sclerotization on posterior surface of each dorsal lobe, from below the lobe base to 1/2 lobe length; a single seta near top of sclerotization, with pale area surrounding its base. Narrow dark brown sclerite often on posterior surface of each lateral lobe, from base to mid-length of lobe. Each ventral lobe roughly triangular in posterior aspect, with subacute tip, basal width 2.5 times length (Fig. 85). Inner surface of each ventral lobe with brown, roughly rectangular sclerite, extending from base to 2/3 length of lobe. Spiracles circular, inner circle black, outer ring brown. A small black circular area between spiracles; remainder of spiracular disc white. Marginal band brown. *Anal Segment:* Four short, rounded anal papillae (Fig. 84),



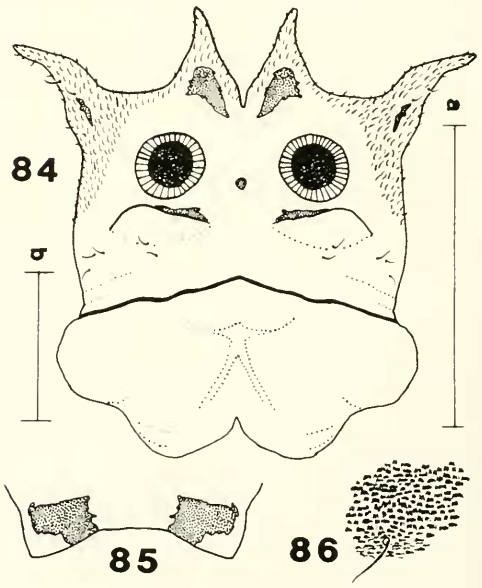
Figs. 81-83. *Tipula (Pterelachisus) trivittata,* abdominal macrosetae. 81, dorsal setae. 82, ventral setae. 83, pleural setae. Scale line 1 mm.

lateral papillae length/basal width approximately 0.50 or less.

Specimens Examined: Thirty-seven larvae from the following localities: ALBERTA: Kananaskis Forest, approx. 80.5 km W of Calgary, H. Teskey, coll. (CNC); KANSAS: Douglas Co., 3.2 km N of Baldwin, J. K. Gelhaus, coll. (JKG); MICHIGAN: Washtenaw Co., Ann Arbor, J. S. Rogers, coll. (UM); same as preceding, G. W. Byers, coll. (KU); NEW YORK: Tompkins Co., Ithaca, C. P. Alexander, coll. (UM); QUEBEC: Gatineau Park, 16.1 km NW of Ottawa (Ontario), H. Teskey, coll. (CNC).

Subgeneric Discussion: *Pterelachisus,* based on *Tipula trivittata* and the descriptions of ten palearctic species, is not distinctly defined by any unique larval characters. The dorsal and lateral spiracular lobes are conical and moderately developed, becoming reduced in the palearctic *T. hortensis* and *T. interposita.* In *T. trivittata,* the sclerotization on the dorsal lobes is present only as an irregular shape near the base of the lobe; the sclerotization on each lateral lobe is a thin line or may be absent. Sclerotization of the dorsal and lateral lobes varies somewhat among the known palearctic species of *Pterelachisus.* In *T. luridirostris,* sclerotization is completely absent, while in *T. meigeni (= hortulana)* and *T. cinercocincta,* it is present as thin vertical strips, resembling the condition in some species of *Vestiplex.* The sclerotization of *T. variipennis* and *T. irrorata* approximates the condition found in *T. trivittata.* The ventral lobes in *Pterelachisus* are broad and low and usually extensively sclerotized on the inner surface. The lateral pair of anal papillae vary from a moderate development in *T. irrorata* to a complete reduction in *T. luridirostris.* Macrosetae D1-D3 and V3-V5 are long and setae D4 and D6 are short, with seta D5 apparently represented only by a socket. In *T. trivittata,* setae V1 and V2 are both short and very close to V3. In *T. irrorata* and possibly other species of *Pterelachisus,* only seta V1 is short. The body is covered with short microscopic hair, arranged in transverse rows, with macroscopic hair generally absent.

The short, conical spiracular lobes of *Pterelachisus* with the small amount of sclerotization on them can be compared to the similar situation in *Serratipula,* some species of *Vestiplex* (e.g., *T. arctica*), *Beringotipula,* and the palearctic *Oreomyza* (sensu Theowald, 1967) and *Dendrotipula.* The small and conical anal papillae, a predominance of short microscopic hairs and similar arrangements of pleural macrosetae are all



Figs. 84-86. *Tipula (Pterelachisus) trivittata.* 84, spiracular area. 85, ventral spiracular lobes, dorsal aspect. 86, example of microscopic hairs on dorsum of abdomen. All scale lines 1 mm. scale a: Fig. 86, scale b: Fig. 84, 85.

seen in *Lunatipula, Vestiplex* and *Serratipula,* as well as in *Pterelachisus.* The arrangement and size of the dorsal and ventral macrosetae are generally the same in all four groups, although in *Pterelachisus* seta D4 is short (long in *Serratipula*) and D5 is apparently absent except for a socket (present as a short seta in the other three groups).

Habitats of *Pterelachisus:* Much of what is known regarding the larval habitats for the over forty nearctic species of *Pterelachisus* pertains to one commonly collected species, *T. trivittata.* Most of the collections of larvae of *T. trivittata* are from well-rotted logs and stumps, generally under the bark or under mosses but occasionally well within the log itself. The logs used are those of deciduous trees. Three collections of *T. trivittata* larvae are of particular interest as the larvae were not found in rotting logs: in Quebec from "ground moss (dry) in oak-maple forest" by H. Teskey (collection label, CNC); in Indiana, "beneath a mixture of *Leucobryum albidum* (moss) and *Bazzania trilobata* (hepatic) on thin soil on sandstone cliff" (Rogers, field notes); in Kansas, at the bases of large oak and hickory trees on a hilltop in a heavily wooded area (Gelhaus, field notes).

Some habitat information is available for a few other nearctic species of *Pterelachisus. Tipula entomophthorae* pupae were collected in North Carolina from humus and decayed wood by G. W. Byers (collection label, KU). J. S. Rogers (1942) writes of *T. angulata,* "A pupal skin of what seems to be this species was taken from a wet aspen log. . . ."

The habitats of European *Pterelachisus* larvae may also give an idea of where the larvae of nearctic species might occur. *Tipula irrorata* larvae have been found under moss on rotten logs or inside the wood, and also in soil under mosses on boulders (Brindle, 1960c). *Tipula interposita, mitophora* and *stenostyla* also inhabit rotten wood under bark or moss (Krivosheina, 1972). *Tipula meigeni (=hortulana)* and *variipennis* have both been found in damp soil in woods (Chiswell, 1956). *Tipula cinereocincta* was collected under moss on tree trunks (Theowald, 1957). *Tipula luridirostris* was collected from the sheaths of reeds (Theowald, 1957) and from unidentified epiphytes growing on oak (Hutson and Vane-Wright, 1969). *Tipula pseudovariipennis* was found under decaying moss (Theowald, 1957).

Subgenus *Savtshenkia* Mannheims

Tipula (Savtshenkia) ignobilis is the only nearctic species of this subgenus for which I have examined reared larvae.

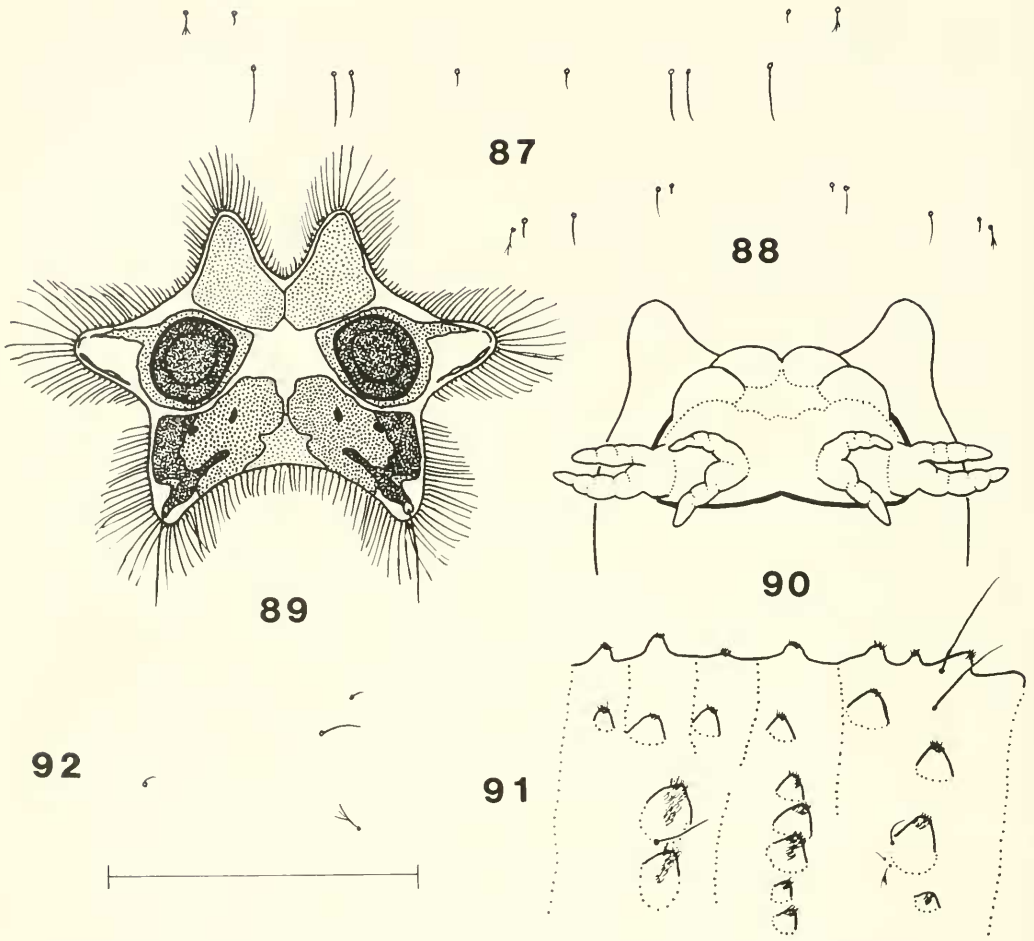
Tipula (Savtshenkia) ignobilis Loew

Alexander 1920:1010-1011, Figs. 511, 530-532.

Description: Length 11.9-17.9 mm, width 1.2-2.6 mm, body brown. *Abdomen:* Most macrosetae dark brown, setae D2-D4 long, D1 and D6 short, D6 pale and branched, D5 very short and inconspicuous (Fig. 87). Seta L2 long, L1, L3 and L4 shorter, L3 pale and branched (Fig. 92). Setae V3 and V4 long, V1 and V2 shorter, V5 very short and inconspicuous, V1 branched (Fig. 88). Abundant macroscopic hairs, densest on dorsum and venter, sparse on pleura. *Spiracular Disc:* All lobes subequal, length slightly greater than basal width, lateral lobes equidistant from dorsal and ventral lobes (Fig. 89). Lobes with well-developed border of setae, longest setae ½ basal width of lobe or less. Posterior surface of each dorsal and ventral lobe with extensive light brown sclerites, often darkest laterally, each ventral lobe also with dark, median line, and two black spots at base. Posterior surface of each lateral lobe with two narrow, lateral light brown sclerites, often extending around margin of spiracles. Spiracles brown, approximately circular; remainder of spiracular disc pale. Marginal band light brown. *Anal Segment:* Eight, subequal anal papillae of medium length, in four pairs (Fig. 90); length/basal width 2.5-4.0.

Specimens Examined: Fifteen larvae from the following localities: MICHIGAN: Washtenaw Co., Cascade Glen, 1.6 km NW of Ann Arbor, G. W. Byers, coll. (KU); NEW YORK: Tompkins Co., Ithaca, C. P. Alexander, coll. (UM); Westchester Co., Armonk, H. Knizeski, coll. (HK).

Subgeneric Discussion: Larvae are known for the nearctic species *Tipula ignobilis* and for fifteen European species. All larval *Savtshenkia* possess four pairs of subequal anal papillae. These papillae show a progression from moderately long and conical as in *T. ignobilis* and *cheethami,* to low



Figs. 87-90, 92. *Tipula (Savtshenkia) ignobilis*. 87, dorsal abdominal macrosetae; width 2 mm. 88, ventral abdominal macrosetae; width 2 mm. 89, spiracular area. 90, anal papillae, ventral aspect. 92, pleural abdominal macrosetae; width 1 mm. Fig. 91. *T. (Savtshenkia)* sp., unreared; abdominal segment, lateral aspect. Scale line 1 mm.

protuberances in *T. pagana* and *obsoleta*. The shape and placement of the spiracular lobes also varies. In *T. ignobilis*, and the *T. rufina* group (sensu Theowald, 1957), the lobes are subequal and moderately long (usually longer than wide), and radially arranged around the spiracular disc. These lobes rest against each other when closed. In other species, such as *T. obsoleta* and *marmorata,* the lobes are generally shorter with the ventral lobes closing against the spiracles, not against the dorsal and lateral lobes. All *Savtshenkia* have a border of setae around the spiracular lobes. At greatest length, in *T. ignobilis* and the *T. rufina* group, the longest setae are at least as long as half the basal width of the lobes. The border of setae is very short in species such as *T. obsoleta, odontostyla* and *marmorata,* with the longest setae less than one-fourth the basal width of the lobes. The amount of sclerotization of the spiracular lobes is also variable. In *T. ignobilis* and other species with moderately long, subequal lobes, the sclerotization is usually extensive, encompassing most of the posterior surface of each lobe. In those species with shorter lobes, the sclerotization extends onto the dorsal and lateral lobes, but only as far as their bases, with the distal areas of the lobes

remaining unsclerotized. These short lobes may be conical or low and rounded; if low, then the ventral lobes are extensively sclerotized.

The two macrosetal arrangements illustrated for the palearctic species (Theowald, 1967) differ in minor details from that of *T. ignobilis*. The *T. rufina* group apparently lacks seta D5, although this seta is found in *T. ignobilis*. In the *T. signata* group, seta D1 is ventrolateral to seta D2, while in *T. ignobilis* it is in the dorsolateral position. *Tipula ignobilis* has a moderate amount of macroscopic hairs, and this apparently is found also in at least *T. alpium* and *marmorata*. Other species, such as *Tipula cheethami*, have predominantly short microscopic hairs.

The number and form of the anal papillae provide a distinctive, synapomorphic character for a subgenus otherwise showing much diversity in larval morphology. The presence of eight, subequal anal papillae is a unique feature in the genus *Tipula*, although *Acutipula* has eight, unequal anal papillae with the two ventral pairs very short. The moderately long, well-developed, subequal spiracular lobes with a border of long setae and with all the lobes closing against one another, as found in *T. ignobilis* and the *T. rufina* group, are similar to their equivalents in the *T. (Trichotipula) oropezoides* group, *Nobilotipula*, and *Schummelia*. The *Tipula signata* group, particularly *T. marmorata* or *obsoleta*, with short spiracular lobes, a border of short setae, and the ventral lobes closing against the spiracles shows resemblance to *Beringotipula* and the palearctic *Nigrotipula* and *Mediotipula* (setal border absent). A general predominance of macroscopic hairs is also found in *T. oropezoides*, but in this species the hairs are denser.

An unreared larva which might be considered within *Savtshenkia* possesses a number of interesting features. Alexander (1920) described this larva from New York as Tipuline no. 1, and I have seen a similar larva from North Carolina. The presence of eight, subequal anal papillae would place it with *Savtshenkia*. It also has moderately long, subequal spiracular lobes with a border of long setae, but possesses many short tubercles on the abdomen, encompassing all the macrosetal bases and numerous in other areas as well (Fig. 91). In addition, most of the apices of the tubercles have clusters of macroscopic hairs. These tubercles are somewhat similar to those of the palearctic *Oreomyza* (sensu Theowald, 1967). The dorsal and lateral spiracular lobes also have a tubercle just before the apex on the anterior, unsclerotized surface. The larvae are conspicuously mottled on the dorsum with patches of dark or light short microscopic hairs, a condition found similarly in some palearctic species of *Savtshenkia*, notably *T. cheethami, simulans* and *goriziensis*.

HABITATS OF *SAVTSHENKIA*: The only habitat information available about the eleven nearctic species of *Savtshenkia* pertains to *T. ignobilis*, where larvae were collected by Alexander (1920) from wet cushions of moss *(Amblystegium)* in New York and also from wet mosses in Maine. In Kansas, Young (1978) collected larvae from "a mat of wet moss on a cliff" and J. A. Slater, Jr. collected pupae from mosses at the base of a limestone cliff where water slowly trickled. G. W. Byers reared larvae in Michigan from "mixed mosses and *Conocephalum* near a small brook. . . . Mosses shaded and on a sandy-marl bank of the brook, where much organic silt also present" (field notes).

Nearly all the palearctic species appear to be associated with mosses, although the specific conditions vary. *Tipula cheethami* has been found "among mosses and liverworts that grow at the edges of streams and on exposed stones and logs in the streams themselves" (Chiswell, 1956). *Tipula macrocera* and *T. subnodicornis* were collected in wet moorland mosses *(Hypnum, Sphagnum* and *Polytrichium)* (Brindle, 1960b), and in cold bogs of tundra and high mountains (Theowald, 1967). Cold bogs and mountain streams are the habitats of *T. goriziensis* (Theowald, 1967). Other species of *Savtshenkia* are found in drier mosses. *Tipula alpium, staegeri*, and *marmorata* are all found in mosses on walls, stones and trees (Brindle, 1960b). *Tipula pagana* is found on and under mosses on soil (Theowald, 1967).

The unreared larva discussed previously (as Tipuline no. 1, Alexander, 1920), was collected in New York from aquatic mosses *(Hypnum)* in a rapidly flowing stream.

Subgenus *Schummelia* Edwards

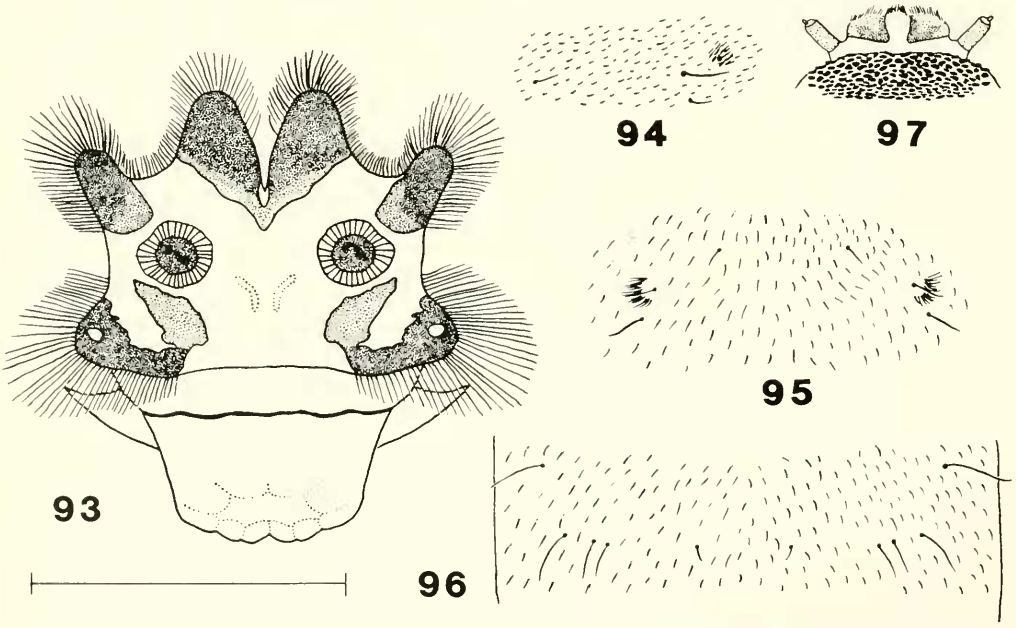
Tipula synchroa is the only nearctic species of *Schummelia* for which the larvae have been associated with adults.

Tipula (Schummelia) synchroa Alexander

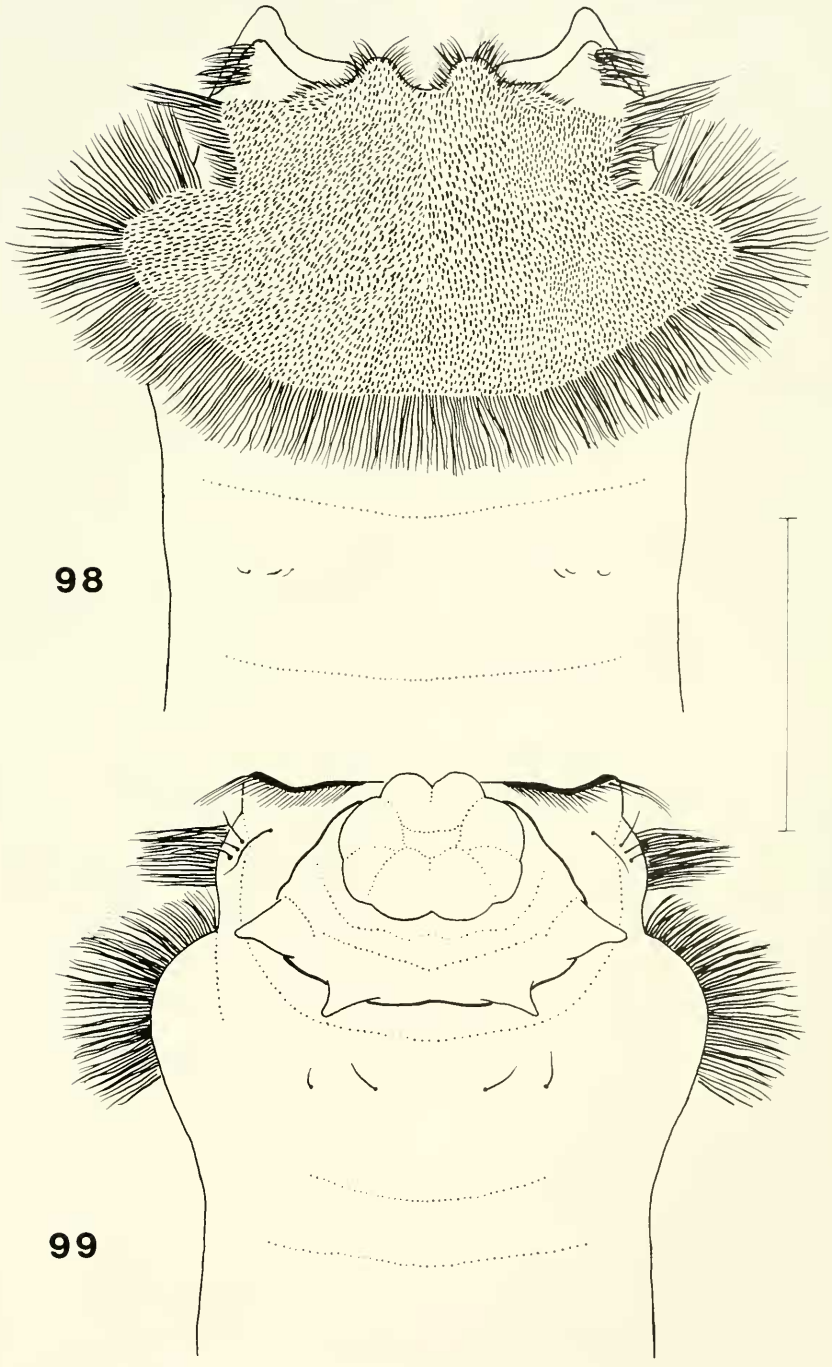
DESCRIPTION: Length 14.3-16.2 mm, width 1.4-1.6 mm, body yellowish brown. Anterior edge of prothorax with thickened cuticle (Fig. 97). *Abdomen:* Most macrosetae brown, setae D2-D4 and D6 long, D1 short, D5 absent, D6 pale (Fig. 96). Seta L2 long, L3 and L4 short, L1 very short and inconspicuous (Fig. 94). Setae V1 and V3 long, V4 short, V2 and V5 absent, V1 pale (Fig. 95). Dorsum of abdominal segment VIII with a semicircular row of long, dark brown macroscopic hairs (Fig. 98); underlying segment with pair of lateral swellings (Fig. 99), microscopic hairs between the hair row and spiracular lobes very short, stout and dark. Other microscopic hairs longer, pale and single. Small tufts of long microscopic hairs around setae L1 and V3, most conspicuous posteriorly. *Spiracular Disc:* All spiracular lobes short, dorsal and lateral lobes as long as width at base, ventral lobes slightly wider than long, lateral lobes equidistant from dorsal and ventral lobes (Fig. 93). Lobes with a well-developed border of setae, longest setae $^2/_3$ basal width of ventral lobe. Border of setae around edges of lobes and between dorsal and lateral lobes, absent between other lobes. Posterior surface of all lobes almost completely covered with dark sclerites; dorsal lobes darkest. Ventral lobe with subapical clear spot, complete sclerite C-shaped. Anterior surface of dorsal and lateral lobes with well-developed subapical clusters of macroscopic hairs. Spiracles subcircular, inner circle dark brown, outer ring brown, distance between spiracles slightly greater than diameter of spiracle. Remainder of spiracular disc pale. Marginal band brown. *Anal Segment:* Segment protuberant; four subequal, single, conical anal papillae (Fig. 99), each as long as wide, anterior and anteriolateral to anus.

SPECIMENS EXAMINED: Nine larvae from Devil's Mill Hopper, 11.3 km NW of Gainesville, Alachua Co., Florida, J. S. Rogers, coll. (UM).

SUBGENERIC DISCUSSION: *Schummelia,* judging by *Tipula synchroa* and the palearctic *T. variicornis,* forms an extremely



Figs. 93-97. *Tipula (Schummelia) synchroa.* 93, spiracular area. 94, pleural abdominal macrosetae and microscopic hairs. 95, ventral abdominal macrosetae and microscopic hairs. 96, dorsal abdominal macrosetae and microscopic hairs. 97, anteriormost area of prothorax and head capsule, dorsal aspect. Scale line 1 mm.



Figs. 98, 99. *Tipula (Schummelia) synchroa,* terminal abdominal segments. 98, dorsal aspect. 99, ventral aspect. Scale line 1 mm.

distinct group. Both species possess the conspicuous, semicircular row of macroscopic hairs on the dorsum of the eighth abdominal segment, with the hairs longest in *T. synchroa*. Additionally, the eighth segment has a pair of protuberances beneath the lateral regions of this hair row. The spiracular lobes are all short with well-sclerotized posterior surfaces, the dorsal lobes most darkly sclerotized. In *T. synchroa*, the anterior surface of the dorsal lobes is unsclerotized and bears subapical clusters of hairs, while in *T. variicornis*, the sclerotization on the posterior surface extends onto the edges of the anterior surface. In both species, the anterior surface of each lateral lobe is covered with macroscopic hairs. The setal border of the spiracular lobes is well-developed, where it occurs, but it is interrupted between the lateral and ventral lobes. In *T. variicornis*, the border of setae is absent entirely from the dorsal lobes. The anal segment is protuberant with four short or moderately long, single papillae. Abdominal seta V2 is absent in both species and V5 and D5 are additionally absent in *T. synchroa*. There are weakly-developed clusters of long microscopic hairs between setae V1 and V3 and around L2. The short microscopic hairs are stouter and dark on the dorsum of the eighth abdominal segment anterior to the spiracular lobes, and closely spaced and appressed on the anterior edge of the prothorax; the remainder of the body is covered with pale microscopic hairs.

The shape, size, placement and sclerotization of the spiracular lobes in *Schummelia*, show a similarity to their equivalents in the *T. (Trichotipula) oropezoides* group. The four, single anal papillae and their placement are also similar to *Trichotipula*. Other subgenera possess four papillae but have the medial pair reduced to rounded, not elongated lobes. Clusters or tufts of hairs can be found in *Beringotipula*, *Tipula* s. str. and *Yamatotipula* as well as in *Schummelia*, with the last subgenus showing the weakest development of this character.

Schummelia shows certain distinct larval characters which make it easy to recognize. The semicircular row of hairs on the eighth segment is unique among the known tipulines, although certain species of *Yamatotipula* (e.g., *T. dejecta*) do have conspicuous clusters of macroscopic hairs near the lateral spiracular lobes. Some aquatic subgenera have dorsal lobes with extensive sclerotization, but *Schummelia*, particularly *T. variicornis*, shows the greatest development of this, with dark sclerotization both anteriorly and posteriorly. The lateral swellings on the eighth abdominal segment, the protuberant anal segment and the loss of certain macrosetae are also distinctive.

HABITATS OF *SCHUMMELIA*: Very little information is available concerning the larval habitats of the seven nearctic species of *Schummelia*. Rogers (1933) recorded the larvae of *T. synchroa* from "wet, black, organic silt of seepage areas" apparently in shaded or heavily wooded situations. Unreared larvae of *Schummelia*, possibly *T. hermannia*, were collected from moist, humous soil in a floodplain woods in Michigan by R. W. Merritt (G. W. Byers, personal communication). *Tipula variicornis* has been collected from "wet leaf mould or wet soil in marshy places or at the edges of ponds and streams, usually in woods" (Chiswell, 1956).

Subgenus *Serratipula* Alexander

I have examined larvae reared and associated with adults of two species of this small subgenus, *Tipula cylindrata* and *graminivora*. Although *T. graminivora* larvae have greater economic importance, *T. cylindrata* larvae are illustrated due to the superior preservation of available specimens.

Tipula (Serratipula) cylindrata Doane

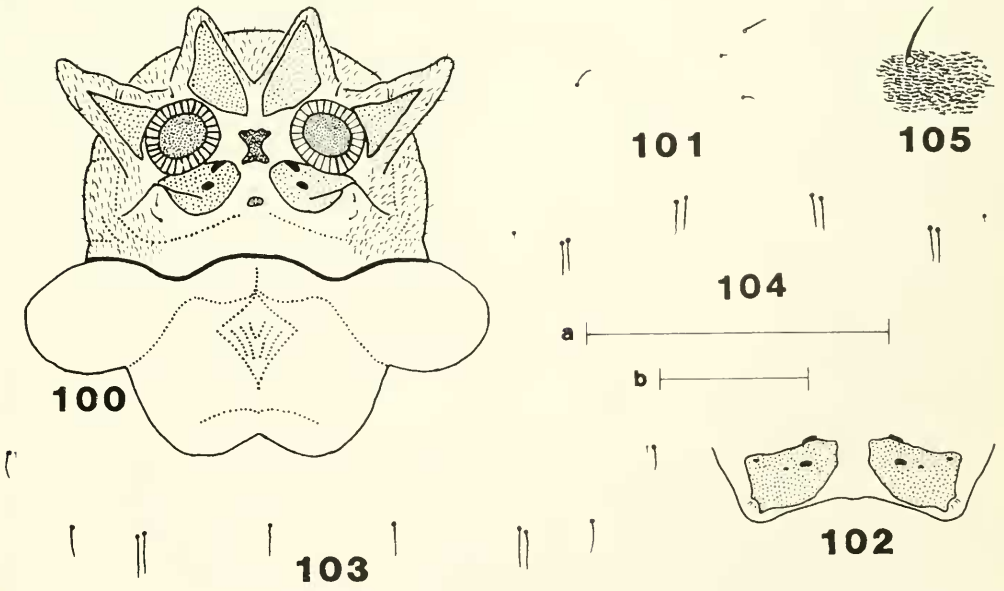
DESCRIPTION: Length 22.1 mm, width 3.6 mm, body light brown. *Abdomen:* Most macrosetae dark brown, setae D1-D4 and D6 long, D5 very short and pale (Fig. 103). Setae L1 and L4 long, L3 short, L2 very short, L1 dorsolateral to L2 (Fig. 101). Setae V2-V5 long, V1 very short and pale (Fig. 104). Short microscopic hairs generally in short, transverse rows on dorsum and venter (Fig. 105), longer microscopic and macroscopic hairs virtually absent; short microscopic hairs on pleura in regularly spaced groups of one to few. *Spiracular Disc:* Dorsal and lateral

lobes subconical, lateral lobes dorsolateral, dorsal lobes ¾ length of lateral lobes (Fig. 100); lobes anteriorly with single long microscopic hairs; a single macroseta between dorsal and lateral lobes, three macrosetae on each lateral lobe at ½ to ¾ length from base. A small seta near tip of each dorsal lobe. A light brown, roughly triangular sclerite posteriorly on each dorsal and lateral lobe, extending from spiracles to near apex. Each ventral lobe broadly triangular in posterior aspect, with subacute tip, basal width 2.5× length; two macrosetae on posterior surface. Inner surface of each lobe with light brown, irregular rectangular sclerite, with four scattered darker spots (Fig. 102). Spiracles circular, evenly brown. An irregular hourglass-shaped brown marking between spiracles; a light brown, oval spot between ventral lobes; remainder of spiracular disc pale. Marginal band brown. *Anal Segment:* Four short, rounded anal papillae (Fig. 100), lateral papillae length/basal width approximately 0.75 or less.

Specimens Examined: Two larvae from La Panza Creek, San Luis Obispo Co., California, C. D. Hynes, coll. (UCR). (One of the larvae is probably third instar and thus was not included in the above length and width measurements.)

Subgeneric Discussion: *Serratipula,* based on *Tipula cylindrata* and *graminivora,* possesses a distinctive combination of characters. The light brown sclerites of the spiracular lobes are extensive, but do not encompass the apices of the lobes. These sclerites are roughly triangular on the dorsal and lateral lobes and more nearly rectangular on the ventral lobes. The spiracles are entirely light brown. The lateral pair of anal papillae is moderately developed in *T. cylindrata.* (The condition of the papillae in *T. graminivora* is not known due to the poor preservation of available material). Seta D4 is long, and the short microscopic hairs are arranged in transverse, short rows.

Serratipula shows similarities in a number of characters to other terrestrial subgenera, such as *Pterelachisus,* the *T. (Lunatipula) bicornis* group and some species of *Vestiplex.* The low, conical, spiracular lobes are most like those of *Pterelachisus.* The extensive sclerotization of the dorsal and lateral lobes is seen similarly in the *T. (Lunatipula) bicornis* group, although the sclerotization on the ventral lobes is most like that in some species of *Pterelachisus* (e.g., *T. trivit-*



Figs. 100-105. *Tipula (Serratipula) cylindrata.* 100, spiracular area. 101, pleural abdominal macrosetae. 102, ventral spiracular lobes, dorsal aspect. 103, dorsal abdominal macrosetae. 104, ventral abdominal macrosetae. 105, example of abdominal microscopic hairs and seta. All scale lines 1 mm. Scale a: Fig. 105, scale b: Figs. 100-104.

tata). A moderate development of the anal papillae is seen, much like the condition found in certain species of *Lunatipula* or *Vestiplex*. Dorsal and ventral setae D1-D3 and V3-V5 are long, and V1 and D5 are short, as in the *T. (Lunatipula) bicornis* group, *Pterelachisus* and *Vestiplex*. Setae D6 and V2 are long, as in the *T. (Lunatipula) bicornis* group.

Certain characters separate *Serratipula* from similar subgenera. Dorsal seta D4 is long, unlike the condition in *Pterelachisus,* the *T. (Lunatipula) bicornis* group, the *T. (Trichotipula) stonei* group, or *Vestiplex*. Seta D6 is long, unlike that of *Pterelachisus* and *Vestiplex*. The spiracles are completely brown in *Serratipula,* whereas, in the above subgenera, the inner circle is black or distinctly dark brown. The extensive sclerotization of the dorsal and lateral lobes is unlike the minor sclerotization found in *Pterelachisus,* the *T. (Trichotipula) stonei* group and certain species of *Vestiplex* (cf., *T. arctica*). The pronounced anal papillae differ from the reduced papillae of the *T. (Lunatipula) bicornis* group and the *T. (Trichotipula) stonei* group.

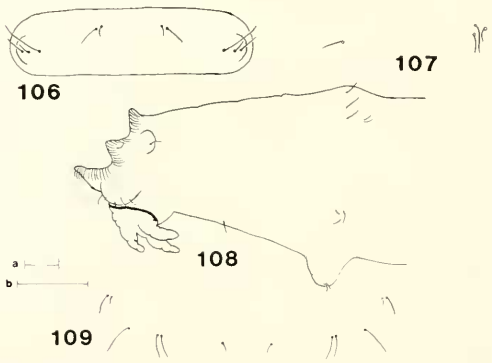
HABITATS OF *SERRATIPULA: Serratipula* is a subgenus of four species. Three of these are found only in California and the fourth occurs both in California and Oregon. Two species, *T. graminivora* and *tristis,* have been recorded as causing economic damage to pasture and rangelands by feeding on grasses (Alexander, 1967). Surprisingly, there have been only brief references to the larval habitats for these two species (Alexander 1921, 1967; Packard and Thompson 1929), and neither of the larvae has previously been illustrated. No habitat information was available with the specimens of *Tipula cylindrata* described above.

Subgenus *Sinotipula* Alexander

Tipula (Sinotipula) commiscibilis is the only species in this group for which the larvae have been associated with adults.

Tipula (Sinotipula) commiscibilis Doane

DESCRIPTION: Length 35.8-51.5 mm, width 5.0-6.4 mm, dorsum with a dark brown background; on each segment with two light brown, lateral longitudinal bands connected by median, transverse, irregular band; 2 pairs of light brown spots anterior to median band, four pairs of light brown spots posterior to band (Fig. 111). Pleura and venter brown. *Abdomen:* Posterior portions of abdominal segments I-VII with conspicuous, ventral transverse swellings (Fig. 108), increasing in height posteriorly, the most developed swellings with basal width twice height. Abdominal segment VIII with circular swellings anterior to but between dorsal and lateral spiracular lobes and anterolateral to each ventral lobe (Fig. 108). Macrosetae dark brown, setae D2-D4 and D6 long, D1 and D5 shorter (Fig. 109). Setae L2-L4 long, L1 shorter (Fig. 107). Setae on transverse swellings, V1, V3 and V4 long, V2 and V5 shorter (Fig. 106). Body with short microscopic hairs, in rows on dorsum and venter, single on pleuron (Fig. 112). Dorsal microscopic hairs forming overall light and dark "H"-pattern as described above; scattered small circular areas without microscopic hairs, surrounded by dark microscopic hairs. Macroscopic hairs absent. *Spiracular Disc:* Lateral and ventral spiracular lobes short, basal width slightly greater than length; dorsal spiracular lobes narrower, as long as wide. Lateral lobes equidistant from dorsal and ventral lobes (Fig. 110). Spiracular lobes with well-developed border of setae, longest setae less than ½ basal width of lobe. Posterior surface of each lobe pale; two to four dark spots at base of each ventral lobe; often a light brown sclerite lateral to spots. Spiracles small, circular, inner circle dark, outer ring brown; distance between spiracles twice or more diameter of spiracle. Marginal band brown. *Anal Segment:* Six, short anal

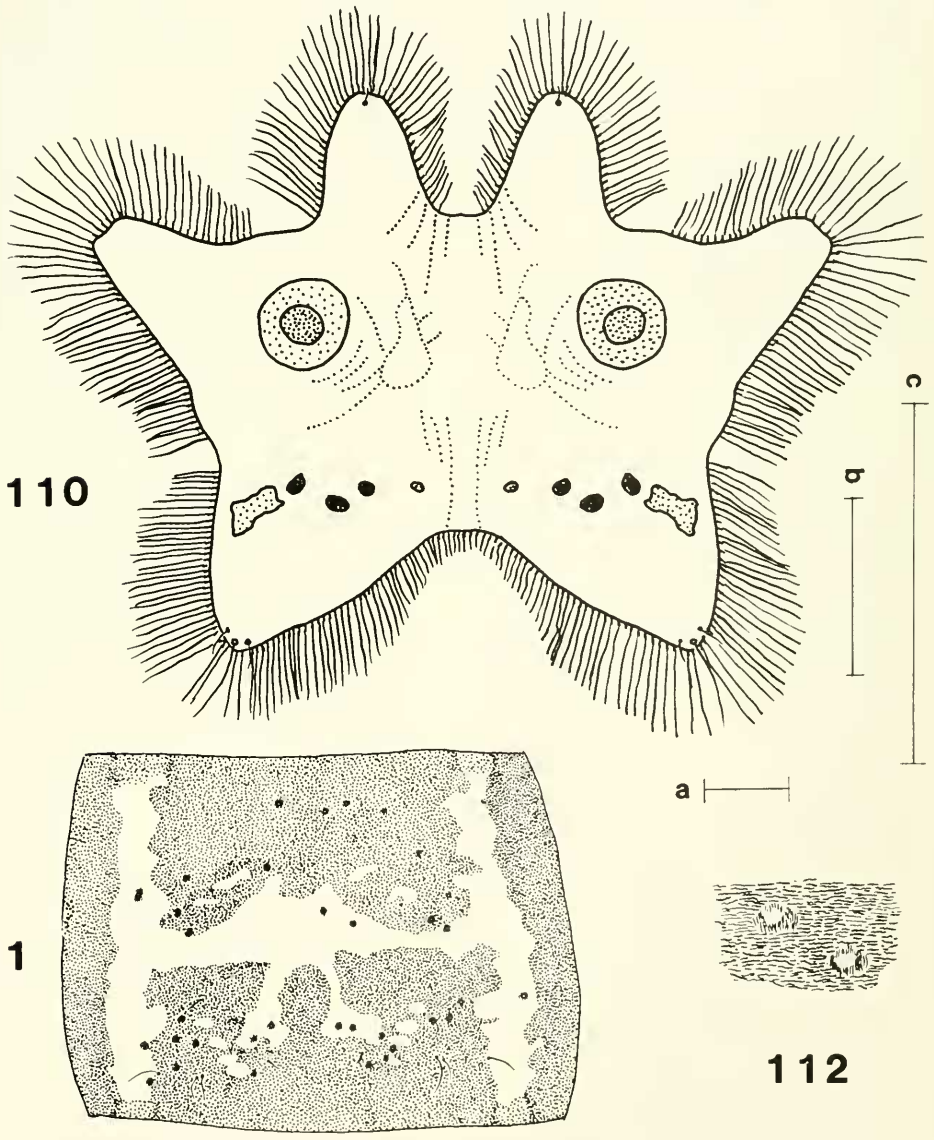


Figs. 106-109. *Tipula (Sinotipula) commiscibilis.* 106, ventral abdominal macrosetae on transverse swelling. 107, pleural abdominal macrosetae. 108, terminal abdominal segments, lateral view. 109, dorsal abdominal macrosetae. All scale lines 1 mm. Scale a: Fig. 108, scale b: Figs. 106, 107, 109.

papillae (Fig. 108), medial papillae paired, lateral papillae single; length/basal width of lateral papilla 2.0-3.0.

SPECIMENS EXAMINED: Four larvae were collected from Big Hill Creek, Big Hill Springs Provincial Park, approx. 33 km NW of Calgary, Alberta, G. Pritchard, coll. (KU).

SUBGENERIC DISCUSSION: *Sinotipula,* as judged by *Tipula commiscibilis,* shows a distinctive combination of features. An obvious character is the presence of ventral transverse swellings on the abdomen, found also in *Nippotipula* and, to a lesser extent, in *Yamatotipula* (specifically, *T. caloptera*). Both *T. caloptera* and *Sinotipula* also possess lateral swellings on abdominal segment VIII and a similar abdominal pattern formed by the dark and light, short micro-



Figs. 110-112. *Tipula (Sinotipula) commiscibilis.* 110, spiracular area. 111, abdominal segment, dorsal aspect. 112, example of microscopic hairs on abdomen. All scale lines 1 mm. Scale a: Fig. 111, scale b: Fig. 110, scale c: Fig. 112.

scopic hairs. Longer microscopic hairs are rare in *Sinotipula* and macroscopic hairs are absent. The spiracular lobes are short and broad with a well-developed border of setae as in other aquatic groups but the posterior surface of each lobe almost completely lacks darkened sclerites. The spiracles are small and widely separated, and the anal papillae are relatively short. None of the macrosetae is branched, although branched setae are found in most aquatic subgenera.

Few larvae of other subgenera could be confused with those of *Sinotipula.* The ventral abdominal swellings, microscopic hair pattern, small spiracles, total lack of macroscopic hairs, broad spiracular lobes and large mature size will serve to separate *Sinotipula* from other aquatic groups. *Yamatotipula* (specifically *T. caloptera*) is most similar in appearance to *Sinotipula,* although a few distinctions can be made between them. Of these, most important is the presence of clusters of macroscopic hairs on *T. caloptera* and the absence of macroscopic hairs in *Sinotipula.* Also lacking in *Sinotipula* is a dark median line on the ventral spiracular lobes, a character which all known larvae of *Yamatotipula* possess.

HABITATS OF *SINOTIPULA: Sinotipula* contains 19 nearctic species, all occurring in western North America. Larvae of *T. commiscibilis* described above were collected from a fairly fast-flowing creek, where they were under completely submerged rocks in the stream bed.

On a number of occasions, I have collected larvae which are very similar to those of *T. commiscibilis,* but I was unsuccessful in the two attempts to rear them. In an extremely fast run between two riffles, of the Cimarron River in Colfax Co., New Mexico, larvae were found under large rocks on the river bed, in water approximately 61 cm deep. They appeared to be the most abundant insect in terms of biomass, and were certainly the most common large insect. I have found larvae at other localities inhabiting similar situations, although not in the abundance seen in the Cimarron River.

Subgenus *Tipula* Linnaeus S. Str.

Only one species of this subgenus, *Tipula paludosa,* occurs in North America. It is an introduced species from Europe.

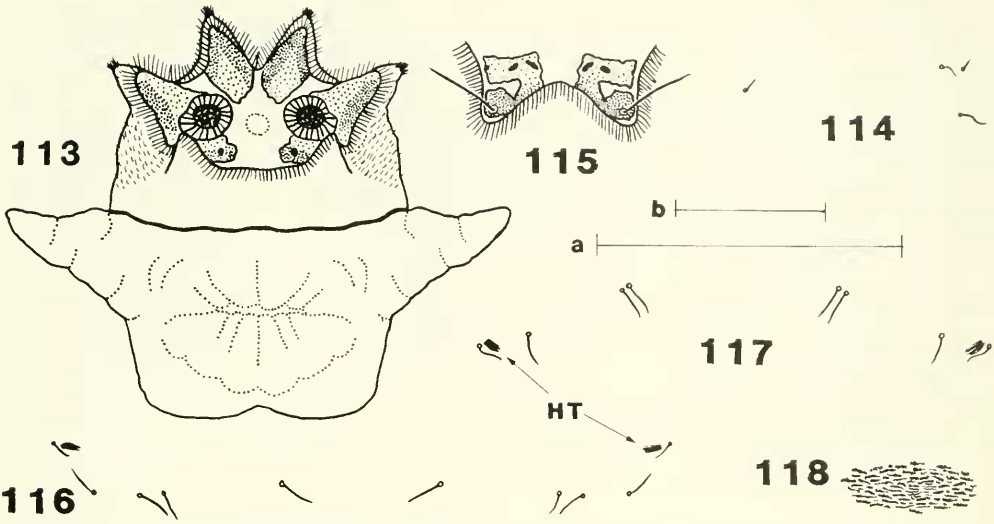
Tipula (Tipula) paludosa Meigen

Selected references: Hennig 1950:410, Figs. 216,222; Chiswell 1956:468-472, Figs. 91-93; Brindle 1960a:176-177, Fig. 1; Theowald 1967:27-28, Figs. 59-61.

DESCRIPTION: Length 23.3-38.0 mm, width 3.7-4.9 mm, body light brown, pleura often darker. Dark tufts of macroscopic hairs at base of each thoracic dorsal macroseta. *Abdomen:* Macrosetae black, all medium length; setae D5 and V2 absent (Figs. 114, 116, 117). Short microscopic hairs in short rows on dorsum and venter (Fig. 118), in groups of one to few hairs on pleura. Dark macroscopic hairs in tufts mediolateral to setae D6 and V1, and anterior to area between dorsal and lateral spiracular lobes, a few isolated hairs near seta D4. *Spiracular Disc:* All lobes subequal, as long as width at base, lateral lobes equidistant from dorsal and ventral lobes (Fig. 113). Lobes with complete border of short setae, longest setae approximately 1/5 basal width of ventral lobe. Most of posterior surface of each dorsal and lateral lobe sclerotized, sclerites darkest laterally. Inner surface of each ventral lobe with dark, C-shaped sclerite, apex darkest, three dark spots at base (Fig. 115). Spiracles roughly circular, inner circle black, outer ring brown; distance between spiracles less than or equal to diameter of a spiracle. Anterior surface of dorsal and lateral lobes with single microscopic hairs; macroscopic hair tufts at apex of each lobe. Marginal band brown. *Anal Segment:* Segment large, anal opening transverse. Four anal papillae (Fig. 113), lateral pair conical, length slightly longer than width at base, ventral pair as broadly rounded protuberances.

SPECIMENS EXAMINED: Over 50 larvae from the following localities in WASHINGTON: Skagit Co.: Mt. Vernon, R. Rosander, coll.; Burlington, J. Crawford and J. Ponnell, coll.; Whatcom Co.: Bellingham, L. Benedict, coll.; Birch Bay State Park, R. Rosander, coll.; Blaine, F. Nonini, coll.; Peace Arch, Knoblauch and Leckie, colls. (all WSU).

SUBGENERIC DISCUSSION: *Tipula paludosa* is an easily recognized larva. The dorsal and lateral spiracular lobes are only sclerotized on the basal three-fourths of each lobe, with the apical fourth remaining unsclerotized. A small apical tuft of mac-



Figs. 113-118. *Tipula (Tipula) paludosa.* 113, spiracular area. 114, pleural abdominal macrosetae. 115, ventral spiracular lobes, dorsal aspect. 116, dorsal abdominal macrosetae, with hair tufts. 117, ventral abdominal macrosetae, with hair tufts; HT-hair tuft. 118, example of microscopic hairs on abdomen. All scale lines 1 mm. Scale a: Fig. 118, scale b: Figs. 113-117.

roscopic hairs is present on each of these lobes. Each ventral lobe is heavily sclerotized on the inner surface and closes against the spiracles, not against the dorsal and ventral lobes. The setae around the spiracular lobes are only of moderate length, but completely border each lobe. A particularly distinctive feature is the dark tufts of macroscopic hairs near abdominal setae V1 and D6, and near the thoracic setae as well. Abdominal setae V2 and D5 are absent (or possibly obscured by the macroscopic hair tufts).

The shape and placement of the spiracular lobes and the border of short setae show a similarity of *Tipula* s. str. to *Yamatotipula* and the non-nearctic *Acutipula.* Both *Acutipula* (*T. vittata* group sensu Theowald, 1957) and *Tipula* s. str. have tufts of macroscopic hairs on the apices of the dorsal and lateral lobes. The subgenera *Yamatotipula, Acutipula, Beringotipula* and *Tipula* s. str. all have patches of macroscopic hairs on the abdomen, although in *Tipula* s. str., these tufts are made up of a few closely set, dark hairs located near the setae, and originating from one small constricted area, differing from the larger clusters of hairs surrounding the setae in the other subgenera. The anal papillae are not elongate as in *Yamatotipula, Platytipula* and most of the other aquatic and semiaquatic groups but are most similar to those found in terrestrial and some semiaquatic groups such as *Beringotipula* and *Lunatipula.* At least one species of *Yamatotipula (T. ludoviciana)* however, has similarly short papillae. The unsclerotized apices and sclerotized bases of the dorsal and lateral lobes in *Tipula* s. str. resemble corresponding parts of the ventral lobes in *Beringotipula,* in which the unsclerotized apex is produced past the sclerotized base.

Tipula s. str. cannot be confused easily with any other subgenus. The general form of the spiracular disc, the complete border of short setae around the spiracular lobes, the small, distinct hair tufts and the small anal papillae make *T. paludosa* distinctive.

HABITATS OF SUBGENUS *TIPULA:* Although *T. paludosa* was accidentally introduced into North America, possibly in ballast from fishing vessels two or three centuries ago, *Tipula* is otherwise an Old World subgenus. The species has become established in Newfoundland and Nova Scotia (Alexander, 1967); recently it has also been found in British Columbia and

Washington (Jackson and Campbell, 1975).

In Europe, *T. paludosa* has been collected from a variety of habitats. Brindle (1960a) found the larvae most common in various pasture soils (peat, clay, sand, marl), but he also collected them in marshy peat soil, in *Hypnum* moss in wet places, and in aquatic mosses through which water slowly trickled. The larvae are well known as pests of many field crops (e.g., barley, rye, wheat) and pastures in Europe, attacking both the roots and shoots (Chiswell, 1956). In North America, based on collection data with the specimens I examined and published reports (Jackson and Campbell, 1975), *T. paludosa* appears to be a pest primarily of turf and pastures.

Subgenus *Trichotipula* Alexander

Of the 34 nearctic species of *Trichotipula,* only two, *Tipula oropezoides* and *T. stonei,* have been reared. The larvae of these species are quite distinct from one another and are discussed separately; in fact, the larvae of both species are at opposite extremes for the entire genus *Tipula* in terms of morpological characters and life histories.

Tipula (Trichotipula) oropezoides Johnson

Alexander 1920:1001-1002, Figs. 506, 513-518.

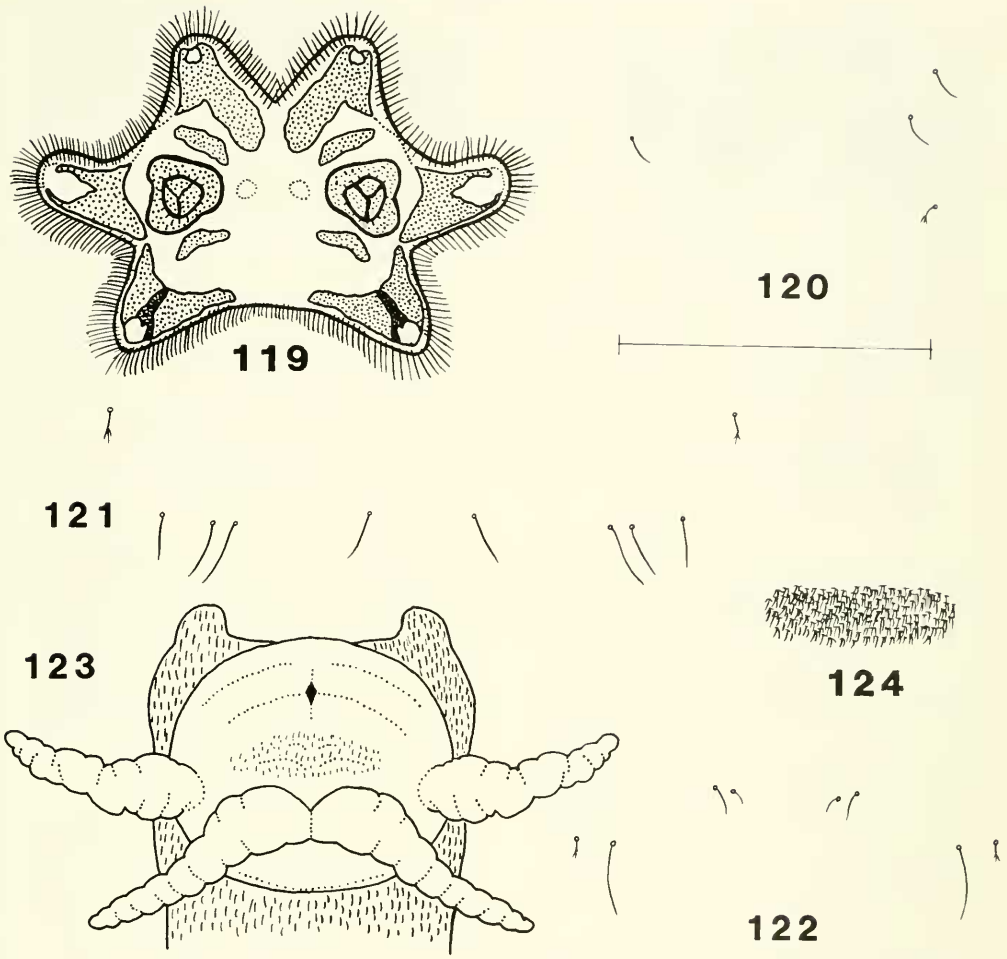
Description: Length 16.7-17.9 mm, width 1.9-2.1 mm, body brown. *Abdomen:* Most macrosetae brown, setae D1-D4 long, D6 shorter pale and branched, D5 absent (Fig. 121). Setae L1, L2 and L4 long, L1 dorsolateral to L2, L3 shorter, pale and branched (Fig. 120). Seta V3 long, V4 of medium length, V1 and V5 short, V1 pale and branched, V2 absent (Fig. 122). Abundant macroscopic hairs, single or in groups of two or three, densest on dorsum (Fig. 124). Microscopic hairs absent. *Spiracular Disc:* All lobes subequal, lobes approximately as long as width at base, lateral lobes equidistant from dorsal and ventral lobes (Fig. 119). Lobes with well-developed border of setae, longest setae ⅓ basal width of lobe. Posterior surface of all lobes with extensive brown sclerites; subcircular pale area at apex of each lobe. Ventral lobe with dark median line. An irregular, transverse brown sclerite above and below each spiracle. Spiracles brown, margins roughly trilobed, inner circle with dark, irregular "Y"-shaped pattern. Remainder of spiracular disc pale. Marginal band light brown. *Anal Segment:* Segment large and circular in ventral aspect; four, elongate anal papillae, with many constrictions along their length (Fig. 123), all papillae single and subequal, length/basal width 2.0-3.5.

Specimens Examined: Six larvae from Needham's Glen, Ithaca, Tompkins Co., New York, C.P.Alexander, coll. (UM, AMNH).

Discussion: Two unique features of *T. oropezoides* are the trilobed spiracles and the small, transverse sclerites located above and below each spiracle. No other *Tipula* is known to possess spiracles which are not circular or at least oval in shape, nor are there such prominent sclerites on the spiracular disc, as the sclerites are usually confined only to the lobes. Also distinctive for *T. oropezoides* are the four elongate anal papillae. In the other species of *Tipula* which have four papillae, these are equally short and conical, as in *Schummelia,* or the median pair is low and rounded, as in *Lunatipula* and some other terrestrial groups. The short spiracular lobes and setal border are similar to these structures in *Schummelia* and some species of *Savtshenkia.* A predominance of macroscopic hairs with an absence of microscopic hairs is seen in *Savtshenkia* (e.g., *T. ignobilis*) as well as *T. oropezoides.* Other taxa, such as *Platytipula, Angarotipula* and the genus *Holorusia,* have an overall "hairy" appearance due to an abundance of macroscopic hairs but microscopic hairs are also present.

Habitats of *Trichotipula* (*oropezoides* group): Alexander (1920) collected larvae of *T. oropezoides* from beneath saturated moss, apparently near the edge of a stream. Rogers (1933) reared the larvae in Florida from "moist to wet clumps of moss, on wet rocks, stream banks and roots." G. W. Byers collected pupae from mixed mosses and liverworts in a floodplain woods in Indiana (field notes).

It is not known how many of the 33 nearctic species of *Trichotipula* will eventually prove to have larvae and larval habitats similar to those of *T. oropezoides* but two species require mention here. Adults of *T. algonquin* were found in wet mossy habitats (Rogers, 1930), and the larvae possibly occur there. Adults of *T. unimaculata* have



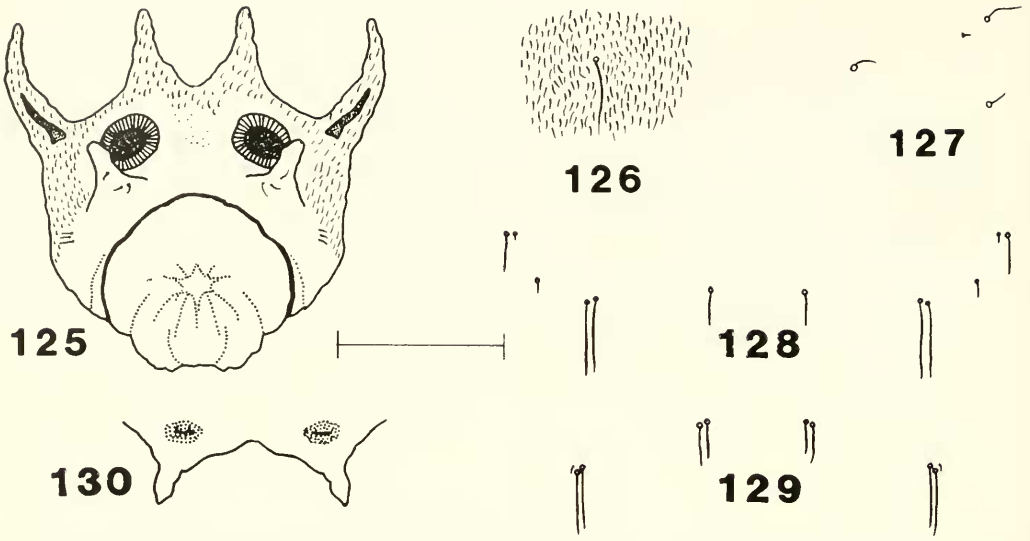
Figs. 119-124. *Tipula (Trichotipula) oropezoides.* 119, spiracular area. 120, pleural abdominal macrosetae. 121, dorsal abdominal macrosetae. 122, ventral abdominal macrosetae. 123, anal papillae, ventral aspect. 124, example of macroscopic hairs on abdomen. Scale line 1 mm.

also been found near wet areas (Rogers, 1942).

Tipula (Trichotipula) stonei Alexander

DESCRIPTION: Length 17.9 mm, width 2.9 mm, body white. *Abdomen:* All macrosetae dark brown, setae D1 and D6 of moderate length, D2 and D3 long, D4 short, D5 vestigial (Fig. 128). Setae L1 and L4 long, L3 of medium length, L2 short, L1 dorsolateral to L2 (Fig. 127). Setae V4 and V5 of moderate length, V2 and V3 long, V1 very short, close to V2 and V3 (Fig. 129). Dorsum and venter with sparse, single long microscopic hairs (Fig. 126); short microscopic and macroscopic hairs absent. Pleura without hairs. *Spiracular Disc:* All lobes conical, dorsal lobes 1.5× as long as width at base; lateral lobes dorsolateral, long, twice length of dorsal lobes; ventral lobes shorter, ⅔ length of dorsal lobes (Fig. 125). Posterior surface of each lateral lobe with thin, dark, medial sclerite, extending from base to midlength of lobe; remainder of lateral lobes and all of dorsal lobes with single, long microscopic hairs. Inner surface of each ventral lobe with light brown circular sclerite at base (Fig. 130). Spiracles approximately elliptical, inner circle black, outer ring brown. Remainder of spiracular area pale and glabrous. Marginal band light brown. *Anal Segment:* Segment small, without distinct papillae.

SPECIMENS EXAMINED: Three larvae from Baldwin Woods, Breidenthal Reserve, 17.7 km



Figs. 125-130. *Tipula (Trichotipula) stonei.* 125, spiracular area. 126, seta and example of abdominal microscopic hairs. 127, pleural abdominal macrosetae. 128, dorsal abdominal macrosetae. 129, ventral abdominal macrosetae. 130, ventral spiracular lobes, dorsal aspect. Scale line 1 mm.

SE of Lawrence, Douglas Co., Kansas, J. K. Gelhaus, coll. (JKG).

DISCUSSION: With a wide base and an elongate, conical form, the ventral spiracular lobes of *Tipula stonei* are distinctive among terrestrial *Tipula* larvae. The inner surface of each of these lobes is unsclerotized except for a light brown spot at the base. The dorsal and lateral lobes also lack appreciable sclerotization; only the posterior surface of each lateral lobe possesses a thin, dark sclerite. The anal segment is small and the anal papillae are not discernible. Single, long microscopic hairs only are on the dorsum and venter; the pleural regions of the abdomen completely lack hairs.

The dorsal and lateral spiracular lobes, each long, and with little sclerotization, are similar to those found in the genus *Nephrotoma* and some species of *Pterelachisus.* This virtual absence of sclerotization contrasts with the more extensive sclerites found in *Vestiplex* and *Lunatipula.* The ventral lobes are much more extended than those found in other terrestrial subgenera. Also striking is the complete absence of any distinct anal papillae in *T. stonei;* this is equivalent only to the condition in the *T. disjuncta* group and *Odonatisca.* Overall, the larva of *T. stonei* shows little similarity to *T. oropezoides,* although they are both placed in the same subgenus.

The larva of *Tipula stonei* can be easily separated from other similar groups. The occurrence of only scattered, long microscopic hairs separates *T. stonei* from other terrestrial subgenera, all of which have a predominance of short microscopic hairs in short rows. The sclerotized, prothoracic welts, unique to the genus *Nephrotoma,* separate it from *T. stonei.*

HABITATS OF *TRICHOTIPULA* (*STONEI* GROUP): Larvae of *T. stonei* were collected under dry leaves in soil 1.3 cm below the surface, on a heavily forested hillside in Kansas, in August. The larvae appear to grow and develop during the hot, dry conditions of summer and do not aestivate or move to moister levels of soil. This is probably significant in terms of the subgenus as a whole, for most of the 33 nearctic species are found in the arid West. It is probable that the larvae of these species will be found in terrestrial situations such as described for *T. stonei,* rather than seepages and wet mosses where *T. oropezoides* has been found.

Subgenus *Triplicitipula* Alexander

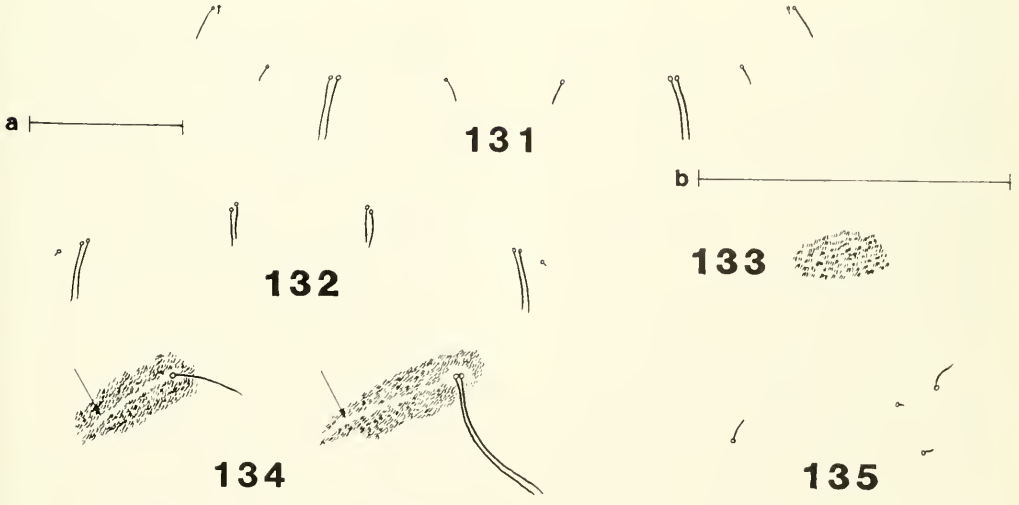
I have examined larvae reared and associated with adults for four species in this subgenus.

Tipula (Triplicitipula) triplex Walker

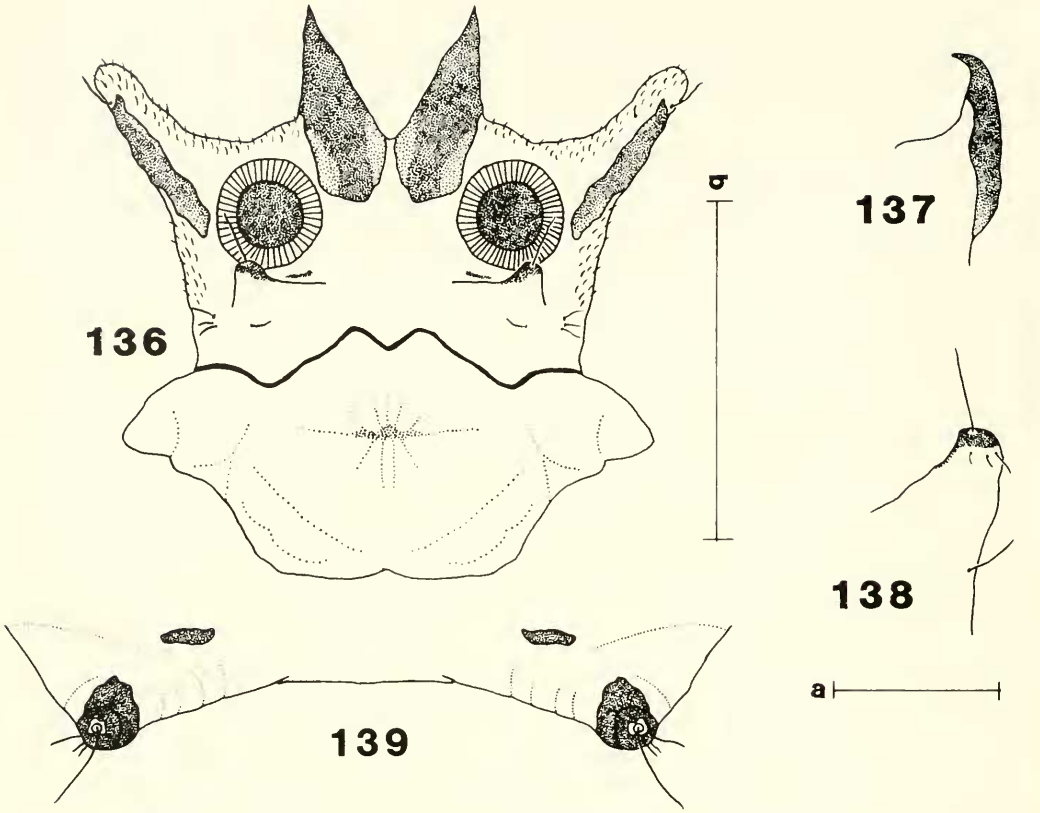
DESCRIPTION: Length: 26.5-32.9 mm, width 3.9-4.6 mm, body brown. *Abdomen:* All macrosetae dark brown to black, setae D2 and D3 long, D6 slightly shorter, D1 and D4 short, D5 very short (Fig. 131). Setae L1 and L4 long, L2 and L3 short and appressed (Fig. 135). Setae V2 and V3 long, V4 and V5 slightly shorter, V1 very short (Fig. 132). Short microscopic hairs in short rows on dorsum and venter (Fig. 133), single on pleura. Microscopic hairs on dorsum dense and longer around bases of setae D1-D4 and on segment VIII; narrow areas without hairs, originating from bases of D1-D3 and extending medioposteriorly for approximately length of setae (Fig. 134). *Spiracular Disc:* Dorsal and lateral lobes subconical, lateral lobes dorsolateral, close to dorsal lobes, lateral lobes slightly longer than dorsal lobes (Fig. 136). Ventral lobes small, short, narrow basally, basal width of each twice its length, apex of each truncated (Fig. 138). Posterior surface of each dorsal lobe with complete, dark sclerite, extending from between spiracles to apex of lobe, distal third of lobe sclerotized anteriorly and posteriorly, apex of lobe an acute, anteriorly directed point (Fig. 137). Posterior surface of each lateral lobe with lateral sclerite, apex of lobe unsclerotized. Distal third of each ventral lobe with dark sclerite, a large seta arising from a pale spot at apex; a black spot at base of lobe (Fig. 139). Spiracles large, circular, outer circle dark brown, inner circle black. Remainder of spiracular disc pale. Marginal band dark brown. *Anal Segment:* Four anal papillae, lateral papillae small, width at base 1.5× length, ventral papillae broadly rounded. Anal opening horizontal.

SPECIMENS EXAMINED: Ten larvae from: KANSAS: Douglas Co., Lawrence, along Kansas River, G.W.Byers, coll. (KU); Douglas Co., Hole-in-the-Rock, 8.0 km W of Baldwin City, J.K.Gelhaus, coll. (JKG); NORTH CAROLINA: Forsyth Co., approximately 6.4 km W of Stokesdale, W.H.Bailey, coll. (NC).

SUBGENERIC DISCUSSION: Larvae have been associated for six species of *Triplicitipula,* four which I have examined *(T. aequalis, integra, praecisa* and *triplex)* and two *(T. acuta, simplex)* described by Hartman and Hynes (1982). Although not unique to *Triplicitipula,* one obvious feature of all of these species is the extensive sclerotization of both the dorsal and lateral lobes. In particular, the sclerites of the dorsal lobes include the apices and form anteriorly directed points. The one known exception is



Figs. 131-135. *Tipula (Triplicitipula) triplex.* 131, dorsal abdominal macrosetae. 132, ventral abdominal macrosetae. 133, example of microscopic hairs on abdomen. 134, abdominal microscopic hairs and seta, showing "setal imprints." 135, pleural abdominal macrosetae. All scale lines 1 mm. Scale a: 131, 132, 135, scale b: 133, 134.



Figs. 136-139. *Tipula (Triplicitipula) triplex.* 136, spiracular area. 137, dorsal spiracular lobe, lateral aspect. 138, ventral spiracular lobe, lateral aspect. 139, ventral spiracular lobes, dorsal aspect. Scale lines 1 mm. Scale a: Figs. 136, 137, scale b: Figs. 138, 139.

T. simplex; in this species, the dorsal lobes are largely sclerotized, but the apices remain unsclerotized. The lateral lobes in *Triplicitipula* are sclerotized only on the lateral half. Each ventral lobe is roughly trapezoidal with a truncated apex and a single, long hair arising from its center. The inner, distal third of this lobe is darkly sclerotized and one or two black spots are located at the base in all the known species. The spiracles are large, circular, and dark. The lateral anal papillae may be slightly developed or absent. The arrangement of the macrosetae is similar in all of the species examined except the length of seta D4 varies; it may be shorter or longer than D2 and D3. The microscopic hairs are short, dark and dense, with conspicuous "setal imprints", that is, bare areas of the cuticle extending medioposteriorly from the base of certain macrosetae which indicate the density of the microscopic hairs.

Triplicitipula is similar in overall form to *Hesperotipula* and both possess truncated, darkly sclerotized ventral lobes and similar densities of microscopic hairs, including "setal imprints". As discussed previously, all studied species of *Triplicitipula* except *T. simplex* have heavily sclerotized dorsal lobes with distinct, curved points at their apices. This is found as well in *Hesperotipula,* some species of *Vestiplex* and most known species *Lunatipula* (*T. fuliginosa* and *T. lunata* groups). However, in *T. simplex* the dorsal lobes with unsclerotized apices are most comparable to the condition in the *T. bicornis* group of *Lunatipula.* Larvae of *Triplicitipula* can be separated from those of most *Lunatipula* by the shape of the ventral lobes. These lobes have a truncate, darkly

sclerotized apex and possess a single, long apical seta in *Triplicitipula;* in *Lunatipula,* the ventral lobes have rounded to only slightly truncated apices, the pattern of sclerotization varies but is not as it is in *Triplicitipula,* and there is never a long, erect, apical seta. Additionally, the microscopic hairs in *Triplicitipula* are longer and more dense than on the *T. fuliginosa* group of *Lunatipula. Hesperotipula* possesses ventral lobes with a shape like those in *Triplicitipula,* but these lack the basal spot. Also, the "setal imprints" in *Hesperotipula* are quite faint, and the rows of microscopic hairs are distinctly separated.

Habitats of *Triplicitipula: Triplicitipula* contains nearly 25 nearctic species. Many of the species are found in grasslands. In California, *T. simplex* and *quaylii* cause serious, localized damage to pasturelands by eating the grass roots and shoots (Hartman and Hynes, 1977; Packard and Thompson, 1921). These two species, along with certain species of *Serratipula,* are commonly called "range crane flies." Others, such as *T. acuta* and *silvestra,* occur in similar habitats but do not appear to cause extensive damage. Larvae of *T. triplex* have been collected in North Carolina in soil under clumps of dead orchardgrass (collection label, NC).

Wooded areas are also inhabited by larvae of *Triplicitipula.* I have collected larvae of *T. integra* in Kansas from wet, sandy soil under leaf litter in a mixed deciduous woods, as well as under accumulations of dry leaves in an open grassy area bordering a woods; *T. triplex* has been reared from similar situations. In California, *T. praecisa* was reared from "decaying leaves" (Alexander, 1967) and I have collected larvae of *T. aequalis* in damp, sandy soil under a 1.3 cm layer of oak, fig and horsechestnut leaves.

Subgenus *Vestiplex* Bezzi

I have examined larvae reared and associated with adults for two species of this subgenus, *Tipula arctica* and *T. platymera.*

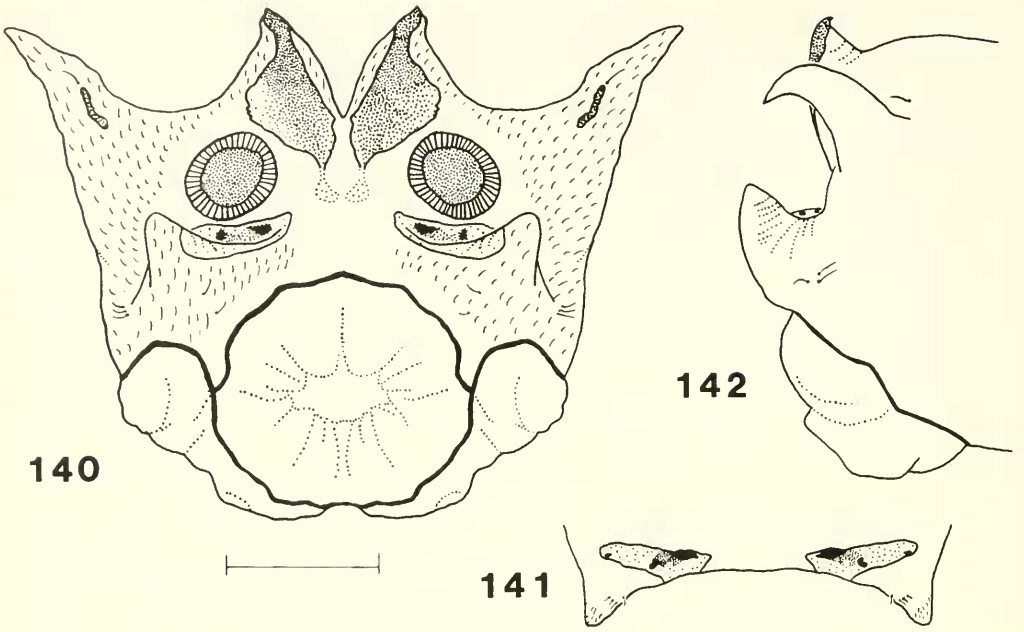
Tipula (Vestiplex) platymera Walker

Teale and Gelhaus 1984:424-427, Figs. 9-16.

Description: Length 26.7-34.9 mm, width 4.3-5.9 mm, body yellowish brown. *Abdomen:* Most macrosetae dark brown, setae D1-D3 long, D4-D6 short and appressed, D5 pale (Fig. 143). Setae L2 and L3 very short, L1 and L4 long, L1 dorsolateral to L2. Setae V2-V5 long, V1 very short (Fig. 144). Short microscopic hairs in long rows on dorsum and venter, single on pleura. *Spiracular Disc:* Dorsal and lateral lobes subconical, lateral lobes dorsolateral; dorsal lobe $^2/_3$ length of lateral lobe (Fig. 140). Ventral lobes small, triangular in posterior aspect, basal width of each approximately twice length of lobe. Posterior surface of each dorsal lobe with irregular sclerite extending from base to apex, apex a short, sclerotized, anteriorly directed point (Fig. 142). Each lateral lobe with thin, dark sclerite, from near base to midlength of lobe. Inner surface of each ventral lobe with three dark basal spots, pale brown sclerite surrounding spots and extending onto outer surface (Fig. 141). Remainder of lobes with single microscopic hairs. Spiracles approximately circular, inner circle black, outer ring brown; a pair of light brown areas between spiracles. Remainder of area around spiracles white and glabrous. Marginal band brown. *Anal Segment:* Four, broadly rounded anal papillae (Fig. 140), a brown band extending between anus and papillae, and connecting to marginal band.

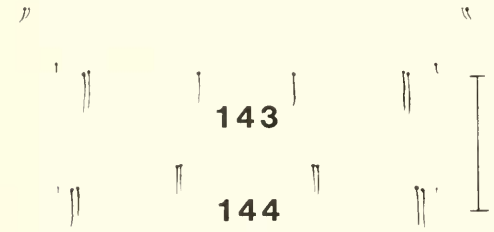
Specimens Examined: Fifteen larvae from Silver Lake, 30 km W of Centennial, Carbon Co., Wyoming, S. Teale, coll. (ST,JKG).

Subgeneric Discussion: Larvae are known for two of the seventeen nearctic species of *Vestiplex,* and for eight palearctic species. The most important synapomorphy seen in all these species is a brown band separating the anus from the anal papillae. This is a unique feature among the subgenera of *Tipula.* The posterior surface of each dorsal spiracular lobe is broadly sclerotized, and in some species, the sclerotization encompasses the apex of the lobe and forms an acute point. In the palearctic *T. virgatula montivaga* each dorsal lobe has a dark sclerite at both the base and apex, with an unsclerotized region separating these two sclerites. Each lateral lobe usually possesses a thin, more or less vertical sclerite, but this may be entirely absent in some species. The ventral lobes are broadly triangular, varying from a moderate development in *T. platymera* and the palearctic *T. scripta,* to scarcely evident in *T. virgatula montivaga.* In most



Figs. 140-142. *Tipula (Vestiplex) platymera.* 140, spiracular area. 141, ventral spiracular lobes, dorsal aspect. 142, terminal abdominal segments, lateral aspect. Scale line 1 mm.

species each ventral lobe has only a narrow band of sclerotization extending across its inner surface. These sclerites are more extensive in *T. scripta* and *leucoprocta,* in which most of the inner surface is dark, and less extensive in *T. kashkarovi* and *virgatula montivaga,* where only a small irregular sclerite is present. The lateral anal papillae are moderately developed in many species, although they are reduced in a few, such as *T. platymera.* The macrosetal arrangement appears to be consistent in those species for which this information could be obtained *(T. platymera, arctica, scripta),* including short setae D4-D6. According to Theowald (1957, 1967) and Alexander (1919), seta V1 is absent in *T. scripta* and *arctica,* but the seta is very reduced in *T. platymera* and may have been overlooked in these other two species. Short microscopic hairs are arranged in rows and cover most of the abdomen; macroscopic hairs are mostly absent.



Figs. 143-144. *Tipula (Vestiplex) platymera.* 143, dorsal abdominal macrosetae. 144, ventral abdominal macrosetae. Scale line 1 mm.

The conical dorsal and lateral spiracular lobes and the reduced, broadly triangular ventral lobes in *Vestiplex* are similar overall to those in *Pterelachisus, Lunatipula* and *Serratipula.* In *T. platymera* and other related species, the dorsal lobes are sclerotized to the apex, being similar to those in most *Lunatipula.* The dorsal lobes in other species of *Vestiplex,* including *T. arctica,* have varying degrees of sclerotization, but the sclerites do not include the apices of the lobes; the lobes are similar to those of *Pterelachisus, Serratipula* and the *T. (Lunatipula) bicornis* group. The lack of appreciable sclerotization of the lateral lobes, and the macrosetal arrangement and size, particularly a short and appressed seta D6, are characteristics shared by both *Vestiplex* and *Pterelachisus.*

One character, the brown band dividing

the anus from the papillae, serves to separate all known *Vestiplex* from other *Tipula*. All other groups possess only the marginal band separating the anal segment from the spiracular disc.

Habitats of *Vestiplex:* The larvae of *T. platymera* were found in soil under a layer of conifer needles, 2.5 to 5.0 cm thick, in a spruce-pine forest (Teale and Gelhaus, 1984). *Tipula arctica* has been reared from soil under *Cassiope* (Nielsen, 1910) in Greenland, and generally in damp soil in arctic areas (Theowald, 1967). The pupae of *T. longiventris* were collected "below the surface of damp friable woodland soil, beneath an inch-deep layer of leaf mold" and a female was found ovipositing in the "leaf mold and soil near the lower edge of an oak-hickory slope" in Michigan (Rogers, 1942). *Tipula bergrothiana* was reared from a pupa collected in a mossy ground cover in a spruce woods in Alaska (G. W. Byers, field notes). Nearctic *Vestiplex* are characteristic of mountainous or more northern regions.

The palearctic *T. scripta* and *T. hortorum* have been reared from moist soil and leaf litter in deciduous woods (Chiswell, 1956; Theowald, 1957). *Tipula nubeculosa* has been found "in soil in coniferous woods" (Chiswell, 1956). *Tipula excisa* and *montana* were both collected in damp tundra soil, in damp mountain meadows and scree slopes (Theowald, 1967). Vtorov and Savchenko (1968) record *T. leucoprocta* from the mossy spruce forest and meadow ecotone in subalpine areas.

Subgenus *Yamatotipula* Matsumura

I have chosen to describe and illustrate *Tipula (Yamatotipula) strepens,* due to the availability of specimens from several areas within its range.

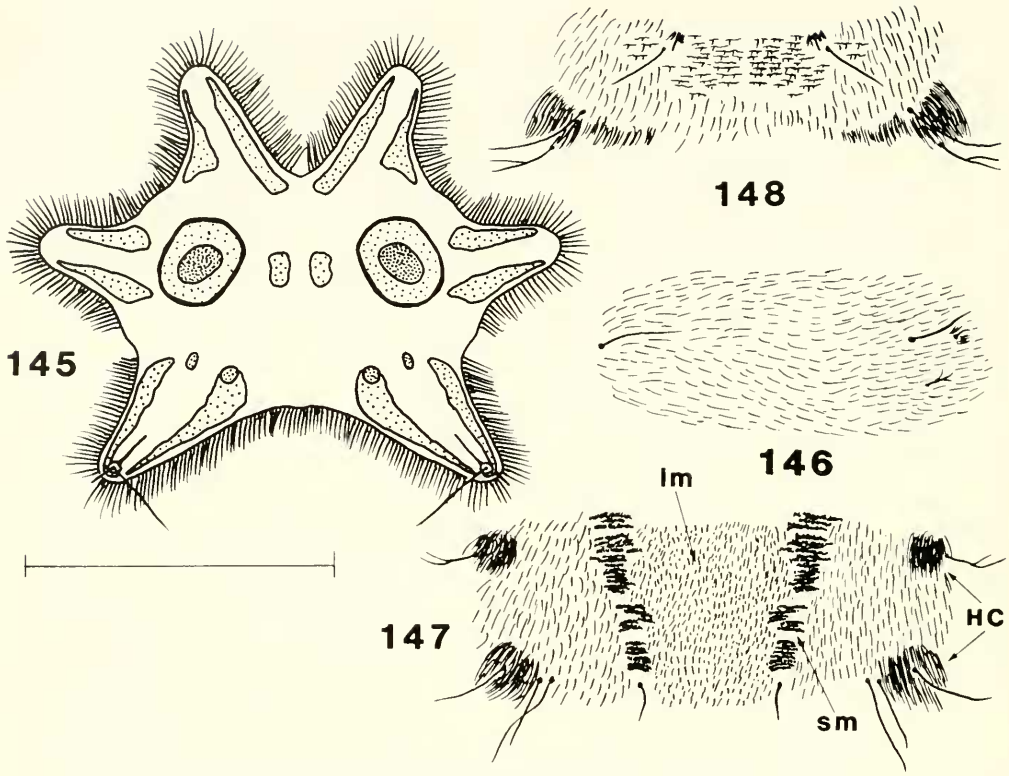
Tipula (Yamatotipula) strepens Loew

Alexander and Byers 1981: Fig. 72.

Description: Length 28.7-34.7 mm, width 3.0-3.9 mm (specimens completely laboratory reared: length 22.3-24.0 mm, width 2.0-2.3 mm), body yellowish-brown. *Abdomen:* Most macrosetae dark brown, setae D2-D4 long, D1, D5 and D6 shorter, D6 pale and branched (Fig. 147). Setae L2 and L4 long, L1 and L3 shorter, L3 pale and branched (Fig. 146). Setae V3 and V4 long, V1 and V2 shorter, V5 very short, V1 pale and branched (Fig. 148). Long and short microscopic hairs and macroscopic hairs present; macroscopic hairs conspicuous, in clusters around setae D4, D5 and V2 (obscuring D5 and V2), on dorsum of segment VIII, and in cluster between dorsal and lateral spiracular lobes. Black short microscopic hairs in long, transverse rows, overall forming two, irregular, longitudinal lines on dorsum (Figs. 147, 151); long microscopic hairs brown and generally distributed. *Spiracular Disc:* All lobes subequal, as long as basal width, lateral lobes equidistant from dorsal and ventral lobes (Fig. 145). Lobes with well-developed border of setae, longest setae 1/3 basal width of lobe. Posterior surface of each lobe usually with two light brown, lateral sclerites. Each ventral lobe with a dark, median line; two dark spots at base. Two macrosetae, one long and one short, at apex of ventral lobe. Spiracles large, approximately circular, inner circle dark brown, outer ring brown; distance between spiracles 1-1.5× diameter of spiracle. Two light brown spots between spiracles may be conspicuous; remainder of spiracular disc pale. Marginal band light brown. *Anal Segment:* Six elongate anal papillae, medial papillae paired, lateral papillae single (Fig. 149), length/basal width of lateral papilla 6.5-8.0.

Specimens Examined: Thirteen larvae from the following localities: KANSAS: Douglas Co., Lawrence vicinity, J. Gelhaus, coll. (JKG); all following collected by H. Teskey (CNC): NEW JERSEY: Montague Co.; NEW YORK: Oswego Co., St. Mary's Pond; Cattaraugus Co., Little Valley, outlet Pigeon Valley Swamp; ONTARIO: Alfred Bog; QUEBEC: Perkins sur le Lac, approx. 21 km NW of Ottawa (Ontario).

Subgeneric Discussion: I have studied associated larvae for 15 of the 50 nearctic species of *Yamatotipula* and know one additional species only from the published description. Larvae have also been described for seven palearctic species. All known *Yamatotipula* have distinct clusters of macroscopic hairs surrounding setae D5 and V2, and on the dorsum of the eighth abdominal segment, anterior to the area between the dorsal and lateral lobes. Often, a distinct cluster is present between setae D2 and D4, surrounding D3. The body also possesses a combination of short and long microscopic hairs. For example, in *T. caloptera* and certain other species, the body is covered almost exclusively with short



Figs. 145-148. *Tipula (Yamatotipula) strepens.* 145, spiracular area. 146, pleural abdominal macrosetae and hairs. 147, dorsal abdominal macrosetae and hairs; HC-hair cluster, lm-long microscopic hairs, sm-short microscopic hairs. 148, ventral abdominal macrosetae and hairs. Scale line 1 mm.

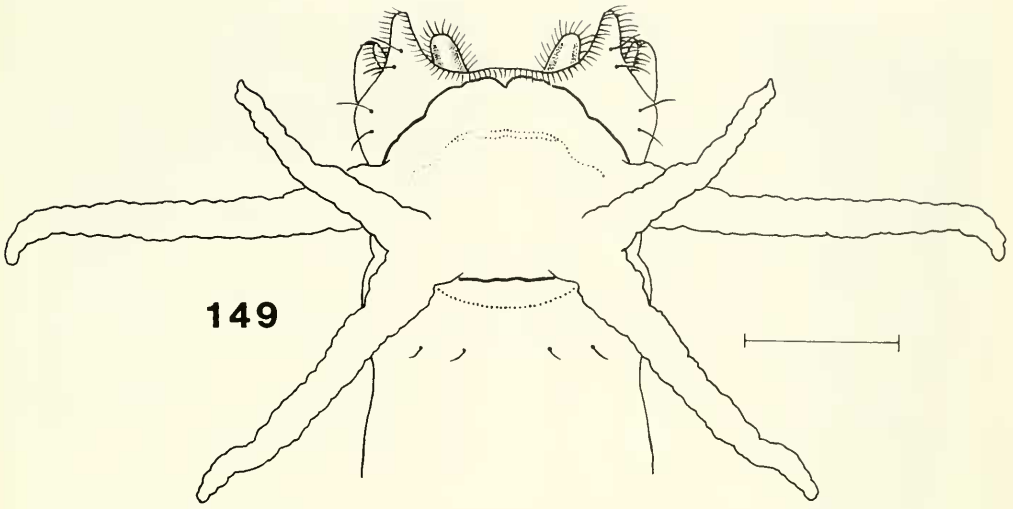
microscopic hairs, organized in rows, with macroscopic hairs only in isolated clusters. In *T. strepens* and others, the long microscopic hairs are more predominant, with macroscopic hairs in clusters. In these latter larval types, the short microscopic hairs are less visible and often distributed in small groups.

The short microscopic hairs may additionally form distinctive patterns. The hairs may be dark and organized into distinct, dorsal stripes (Fig. 151) as found, for example, in *T. strepens.* In *T. caloptera* the combination of light and dark short microscopic hairs forms a distinct pattern of spotting on the dorsum (Fig. 150). The palearctic *T. pruinosa* group and nearctic *T. sulphurea* have a distinct pattern formed by paired, transverse rows of macroscopic hair tufts on the anterior portions of the abdominal segments, in addition to the tufts around the macrosetae. Many species of *Yamatotipula,* however, have no distinct hair patterns.

The spiracular lobes are all approximately equal in length, usually as long as wide, with a well-developed border of setae. The spiracles are large and oval to circular in shape. Although the patterning on the posterior surfaces of the lobes varies among the species examined, often the lobes have darker, lateral sclerites. All *Yamatotipula* known have a dark median line on each ventral lobe.

Six anal papillae are present in most species. Two pairs of papillae are usually long, with the anteriomedial pair often shortened. In some species this shortened medial pair is absent and only four papillae are present. For example, the palearctic *T. solstitialis* has only four long papillae. The nearctic *T. ludoviciana* has only four short papillae.

In *T. caloptera* there are very reduced,



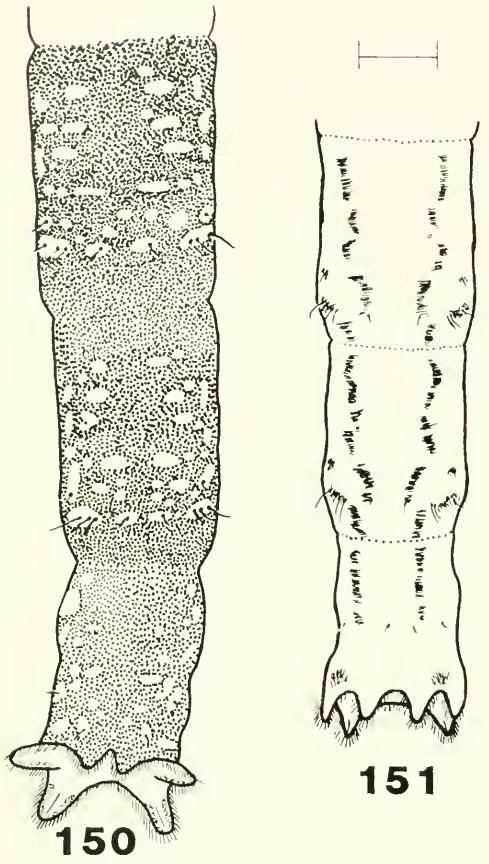
Figs. 149. *Tipula (Yamatotipula) strepens.* Anal papillae, ventral aspect. Scale line 1mm.

transverse abdominal swellings.

Yamatotipula shows similarities to other aquatic and semiaquatic subgenera. The radially arranged, subequal, spiracular lobes with a well-developed border of setae, branched setae D6, L3 and V1, and long anal papillae are characters shared by many aquatic and semiaquatic groups such as *Platytipula, Bellardina,* and *Nobilotipula.* The clusters of macroscopic hairs near macrosetae D5 and V2 are found also in *Beringotipula* and the non-nearctic *Acutipula. Tipula* s. str. has similarly placed patches of macroscopic hairs but they are very dark, few in number, and do not surround the setae, thus forming discrete tufts rather than the more diffuse clusters of *Yamatotipula.* The predominance of short microscopic hairs in a pattern of light and dark areas and transverse abdominal swellings seen in *T. caloptera* are found also in *Sinotipula.*

The distinct, longitudinal microscopic hair patterns as in *T. strepens* and other species and the transverse macroscopic hair patterns found in *T. sulphurea* are unique for *Yamatotipula,* and the larvae cannot be confused with those in any other known group. *Tipula caloptera* also has a distinct abdominal pattern which can only be confused with that of *Sinotipula. Tipula caloptera,* though, possesses macroscopic hair clusters and long anal papillae, while these clusters of hairs are absent and the papillae are short in *Sinotipula.* Species of *Yamatotipula* that lack these distinct patterns can be separated from the similar subgenera *Platytipula* and *Bellardina* and the genus *Holorusia* by the distinct clusters of hairs. *Tipula ludoviciana* has four, short, anal papillae and might be confused with *T. (Tipula) paludosa.* The ventral papillae in *T. ludoviciana,* however, have pointed apices while in *T. paludosa,* they are reduced to low, rounded protuberances; the patches of hairs are different in *Yamatotipula* and *Tipula* s. str. as discussed previously.

HABITATS OF *YAMATOTIPULA:* Larvae of *Yamatotipula* are found in a wide variety of aquatic and semiaquatic situations. Larvae of *T. strepens* are "semiaquatic in the moss and algal mats of the rills and trickles" (Rogers, 1942), and H. Teskey collected this species from wet mosses on stream banks (collection label, CNC). *Tipula caloptera* is recorded from Florida in "wet or submerged mats of mosses and algae" (Rogers, 1933), and I have collected the larvae from mosses in a cold spring-fed stream in Kansas. Rogers (1933) also notes that in *T. caloptera* the "larvae can live for months wholly submerged in well-aerated streams." A pupal skin of *T. brevifurcata* "projected from the wet mosses and algae



Figs. 150-151. *Tipula (Yamatotipula)* spp. 150, *T. (Y.) caloptera,* terminal abdominal segments, dorsal aspect. 151, *T. (Y.) strepens,* terminal abdominal segments, dorsal aspect. Scale line 1 mm.

at the brink of a small shaded falls" (Rogers, 1930). *Tipula concava* has been collected in Tennessee from the coarse sand about the roots of *Dianthera (=Justicia) americana* at the water's margin (Rogers, 1930), although I have collected it in Kansas from exposed tree root clumps and in leaf debris at stream edges. These stream margins are where I have commonly collected larvae of *T. furca,* either in wet, decaying leaf debris or in the sand and muck at the stream edge. Hynes (1957) notes that the larvae of *T. fraterna* are found in damp, steep, stream banks, which are usually covered with mosses and liverworts. In Kansas, I have found *T. tricolor* in leaf debris or mosses from springs and spring-fed streams.

Many larvae of *Yamatotipula* have been recorded from marshy areas with much silt and organic debris. *Tipula furca, sulphurea* and *subeluta* have been reared from the muddy margins of pools (Rogers 1933, 1942). *Tipula dejecta* was collected in thick organic matter in an alder swamp (Alexander, 1920). Rogers (1933) records a number of species, for example, *T. manahatta,* from "wet plastic soils of grass and sedge marshes." The larva of *T. footeana* was found among grass roots on an unshaded mudflat surrounding a lake in Idaho (Foote, 1963).

The known habitats of seven palearctic species are similar to those discussed here.

LITERATURE CITED

ALEXANDER, C. P. 1919. The crane-flies collected by the Canadian Arctic Expedition, 1913-1918. Report Canad. Arctic Exped., 1913-1918, Vol. III: Insects; Pt. C: Diptera: 3c-30c.

———. 1920. The crane-flies of New York. Part II. Biology and Phylogeny. Cornell Univ. Agr. Exp. Sta., Mem. 38: 691-1133.

———. 1921. A new species of *Tipula* injurious to pasturelands (Tipulidae, Diptera). Ins. Insc. Mens. 9: 135-137.

———. 1923. Diptera, suborder Orthorhapha, Division Nematocera. Families Tipulidae and Rhyphidae. *In* A biological survey of the Pribilof Islands, Alaska. Pt. II. Insects, Arachnids and Chilopods of the Pribilof Islands, Alaska. U. S. Dept. Agr. Bur. Biol. Surv., N. A. Fauna. No. 46: 159-169.

———. 1965. New subgenera and species of crane-flies from California (Diptera: Tipulidae). Pacific Insects 7: 333-386.

———. 1967. The crane flies of California. Bull. Calif. Insect Surv. 8: 1-269.

ALEXANDER, C. P. and G. W. BYERS. 1981. Tipulidae. pg. 153-190. *In* J. F. McAlpine and others (eds.), Manual of Nearctic Diptera. Vol. 1. Agr. Canada Monog. No. 27. 674pp.

BRINDLE, A. 1957. The ecological significance of the anal papillae of *Tipula* larvae (Dipt., Tipulidae). Entomol. Month. Mag. 93: 202-204.

———. 1959. Notes on the larvae of the British Tipulinae (Dipt., Tipulidae). Part 4. The

larvae of *Tipula luteipennis* Mg., and *T. melanoceros* Schum. Entomol. Month. Mag. 95: 36-37.

———. 1960a. Notes on the larvae of the British Tipulinae (Dipt., Tipulidae). Part 6. The larvae of the *Tipula oleracea* group. Entomol. Month. Mag. 95: 176-177.

———. 1960b. Notes on the larvae of the British Tipulinae (Dipt., Tipulidae). Part 7. The larvae of the *Tipula marmorata* group. Entomol. Month. Mag. 95: 204-205.

———. 1960c. The larvae and pupae of the British Tipulinae (Dipt., Tipulidae). Trans. Soc. Brit. Entomol. 14: 63-114.

BYERS, G. W. 1961. The crane fly genus *Dolichopeza* in North America. Univ. Kansas Sci. Bull. 42: 665-924.

CAUDELL, A. N. 1913. Notes on the yellow crane-fly, *Tipula flavicans* Fabr. Proc. Entomol. Soc. Wash. 15: 45-46.

CHISWELL, J. R. 1955. On the last instar larva of *Tipula livida* Van der Wulp (Diptera, Tipulidae) with notes on the frontal-clypeal region of larval Tipulinae and caterpillars. Proc. Roy. Entomol. Soc. London (A), 30: 127-136.

———. 1956. A taxonomic account of the last instar larvae of some British Tipulinae (Diptera: Tipulidae) Trans. Roy. Entomol. Soc. London 108: 409-484.

FOOTE, B. A. 1963. Observations on the biology of *Tipula footeana* Alexander (Diptera: Tipulidae). Bull. Brooklyn Entomol. Soc. 58: 145-150.

FORBES, S. A. 1890. The meadow maggots or leatherjackets. Illinois St. Entomol. Rept. 16 (1887-88): 78-83.

GELHAUS, J. K. 1983. The larvae of the crane fly genus *Tipula* in North America. Univ. Kansas, Masters Thesis, 193pp.

GREENE, C. T. 1909. Description of larva and pupa of *Tipula trivittata* Say. Entomol. News 20: 289-290.

HALL, H. A. and G. PRITCHARD. 1975. The food of larvae of *Tipula sacra* Alexander in a series of abandoned beaver ponds (Diptera: Tipulidae). J. Anim. Ecol. 44: 55-66.

HARTMAN, M. J. and C. D. HYNES. 1977. Biology of the range crane fly, *Tipula simplex* Doane (Diptera: Tipulidae). Pan-Pacific Entomol. 53: 118-123.

———. 1982. The immature stages of *Tipula simplex* Doane and *Tipula acuta* Doane (Diptera: Tipulidae). Pan-Pacific Entomol. 58: 153-158.

HEMMINGSEN, A. M. 1958. Adaptations in *Tipula (Lunatipula) lesnei* Pierre to the dry climate of Gran Canaria. Vidensk. Medd. fra Dansk naturh. Foren. 120: 207-236.

———. 1959. A crane-fly living in blown sand. Entomol. Medd. 29: 46-64.

HENNIG, W. 1950. Die Larvenformen der Dipteren. 2. Teil. Akademie-Verlag, Berlin, 458pp.

HOFSVANG, T. 1979. The larvae of *Tipula (Arctotipula) salicetorum* Siebke, 1870 (Diptera: Tipulidae). Entomol. Scand. 10: 238-240.

HUTSON, A. M. and R. I. VANE-WRIGHT. 1969. Corrections and additions to the list of British Nematocera (Diptera) since Kloet and Hincks' "A checklist of British Insects" (1945). Entomol. Gaz. 20: 231-256.

HYSLOP, J. A. 1910. The smoky crane-fly. Bull. U. S. D. A., Bur. Entomol. 85: 19-32.

HYNES, C. D. 1957. A study of the *Tipula fraterna* complex in the southeastern United States (Tipulidae: Diptera). Univ. Florida, Ph.D. Thesis, 139pp.

JACKSON D. M. and R. L. CAMPBELL. 1975. Biology of the European crane fly, *Tipula paludosa* Meigen, in western Washington. Wash. St. Univ. Tech. Bull. No. 81. 23pp.

KRIVOSHEINA, N. P. 1972. Ecology of xylobiontic larvae of Tipulidae. Soviet J. Ecol. 3: 45-52.

MALLOCH, J. R. 1917. A preliminary classification of Diptera, exclusive of Puparia, based upon larval and pupal characters, with keys to imagines in certain families. Part 1. Bull. Illinois St. Lab. Nat. Hist. 12: 161-407.

NEEDHAM, J. G. 1903. Some new life histories of Diptera. pg. 279-287. *In* J. G. Needham and others (eds.), Aquatic Insects in New York State. Bull. New York St. Mus. No. 68.

NIELSEN, J. C. 1910. A catalogue of the insects of north-east Greenland with description of some larvae. *In* The insects of the Danmark expediton. Medd. Gronland 43(2): 55-68.

PACKARD, C. M. and B. G. THOMPSON. 1921. The range crane flies in California. U. S. D. A., Dept. Circ. No. 172. 8pp. (revised 1929).

PRITCHARD, G. 1976. Growth and development of larvae and adults of *Tipula sacra* Alexander (Insecta: Diptera) in a series of abandoned beaver ponds. Can. J. Zool. 54: 266-284.

———. 1978. Study of dynamics of populations of aquatic insects: the problem of variability in life history exemplified by *Tipula sacra* Alexander (Diptera; Tipulidae). Verh. Internat. Verein. Limnol. 20: 2634-2640.

———. 1980. Life budgets for a population of *Tipula sacra* (Diptera; Tipulidae). Ecol. Entomol. 5: 165-173.

———. 1983. Biology of Tipulidae. Ann. Rev. Entomol. 28: 1-22.

PRITCHARD, G. and H. A. HALL. 1971. An introduction to the biology of craneflies in a series of abandoned beaver ponds, with an account of the life cycle of *Tipula sacra* Alexander (Diptera; Tipulidae). Can. J. Zool. 49: 467-482.

PRITCHARD, G. and M. STEWART. 1982. How cranefly larvae breathe. Can. J. Zool. 60: 310-317.

ROGERS, J. S. 1930. The summer crane-fly fauna of the Cumberland Plateau in Tennessee. Occ. Papers Univ. Michigan Mus. Zool., No. 215. 50pp.

———. 1933. The ecological distribution of the crane-flies of northern Florida. Ecol. Monog. 3: 1-74.

———. 1942. The crane flies (Tipulidae) of the George Reserve, Michigan. Misc. Publ. Univ. Michigan Mus. Zool., No. 53. 128pp.

SAVCHENKO, E. N. 1954. On characteristics differentiating larvae of the most common species of crane flies (Diptera, Tipulidae). Zool. Zh. 33: 616-636 [in Russian].

———. 1961. Crane-flies (Tipulidae). Fauna U. S. S. R., Vol. 2, Pt. 3: 1-488 [in Russian].

———. 1964. Crane-fies (Tipulidae). Fauna U. S. S. R., Vol. 2, Pt. 4: 1-504 [in Russian].

TEALE, S. A. and J. K. GELHAUS. 1984. Natural history and synonymy of *Tipula (Vestiplex) platymera* Walker (Diptera: Tipulidae) with descriptions of the larvae and pupae. J. Kansas Entomol. Soc. 57: 423-429.

TESKEY, H. J. 1981. Morphology and Terminology-Larvae. pg. 65-88. *In* J. F. McAlpine and others (eds.), Manual of Nearctic Diptera. Vol. 1. Agr. Canada Monog., No. 27. 674pp.

THEOWALD, B. 1957. Die Entwicklungsstadien der Tipuliden (Diptera, Nematocera), insbesondere der West-Palaearktischen Arten. Tijdschr. Entomol. 100: 195-308.

———. 1967. Familie Tipulidae, (Diptera, Nematocera), Larven and Puppen. Bestimmungsbucher zur Bodenfauna Europas 7: 1-100. Akademie-Verlag, Berlin.

THEOWALD, B. and G. THEISCHINGER. 1979. German translation of "Phylogeny and Systematics of the Tipulidae by E. N. Savchenko, 1966, Fauna Ukraine 14 (1): 63-88." Tijdschr. Entomol. 122: 91-126.

VTOROV, P. P. and E. N. SAVCHENKO. 1968. The immature stages of three species of *Vestiplex* Bezzi (Diptera, Tipulidae) from the highlands of Tien Shan. Vest. Zool. 1: 45-63 [in Russian, English summary].

YOUNG, C. W. 1978. Comparison of the crane flies (Diptera: Tipulidae) of two woodlands in eastern Kansas, with a key to the adult crane flies of eastern Kansas. Univ. Kansas Sci. Bull. 51: 407-440.

———. 1981. The immature instars of *Tipula (Platytipula) ultima* Alexander (Tipulidae, Diptera). J. Kansas Entomol. Soc. 54: 409-415.